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Coastal Ecological Systems of the United States

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edited by

H. T. Odum B. J. Copeland E. A. McMahan

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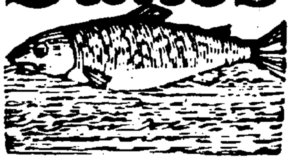
Coastal Ecological Systems of the United States



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Preface

Coastal Ecological Systems of the United States was originally prepared for the Federal Water Pollution Control Administration as part of the National Estuarine Pollution Survey conducted in 1968 and 1969. It was the product of a group of scientists led by staff members of the University of North Carolina's Institute of Marine Sciences. Its four volumes include a comprehensive survey of scientific information through 1969, as well as a new system for the classification of coastal ecosystems. The manuscript was submitted to the U.S. Environmental Protection Agency (which absorbed the FWPCA in 1970), but was not published.

The Conservation Foundation is now able to publish this work because of an assistance grant (Grant No. 043-158-68) provided by the National Oceanic and Atmospheric Administration's Office of Coastal Environment, which is responsible for implementing the Coastal Zone Management Act of 1972. The purpose of the grant was to assist the Conservation Foundation in preparing an amended version of this comprehensive work for NOAA's program use. Upon completion of that activity, the Conservation Foundation agreed to make this material available to a wider audience by reproducing the amended manuscript in the most inexpensive way possible.

Those whose personal efforts merit recognition are Robert W. Knecht, director, and Edward T. LaRoe, coastal ecologist, of the Office of Coastal Environment, who foresaw the relevance of this work to the practical needs of coastal zone management; Eugene T. Jensen and A. L. Wastler, of the U.S. Environmental Protection Agency, who arranged for the original study; and John Clark and Laura O'Sullivan of the Conservation Foundation, who, respectively, persuaded their organization to publish this massive work and attended to the myriad details of bringing it into print.

The Editors:

H. T. Odum,
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CONTENTS

VOLUME ONE

Introduction..1

Acknowledgement...4

Part I A Functional Classification of the Coastal Ecological Systems, H.T. Odum and B.J. Copeland...................................5

Part II Foraminifera in Estuarine Classification, Maynard Nichols..........85

Part III A. Ecological Systems by State, B.J. Copeland and H.T. Odum.......104
B. Coastal Ecosystems of Alaska, C.P. McRoy and J.J. Goering......124

Part IV General Recommendations...132

Part V Chapters on Types of Ecological Systems

A. Naturally Stressed Systems of Wide Latitudinal Range

A-1. Rocky Sea Fronts and Intertidal Rocks, Staff.............152
A-2. High Energy Beaches, Rupert Riedl and Elizabeth A. McMahan...180
A-3. High Velocity Ecosystems, Staff.........................252
A-4. Oscillating Temperature Channels and Canals, Staff.......271
A-5. Sedimentary Deltas, Bruce Nelson........................278
A-6. Hypersaline Lagoons, B.J. Copeland and Scott W. Nixon...312
A-7. Marine Blue-green Algal Mats, Larry Birke................331

B. Natural Tropical Ecosystems of High Diversity

B-1. Mangrove Swamp Systems, Edward J. Kuenzler...............346
B-2. Coral Reefs, Louis DiSalvo and H.T. Odum.................372
B-3. Tropical Marine Meadows, H.T. Odum......................442
B-4. Tropical Inshore Plankton Systems, James A. Marsh, Jr....488
B-5. Tropical Blue-Water Coasts, W.P. Odum and John J. Walsh...514

CONTENTS OF OTHER VOLUMES

VOLUME TWO:

C. Natural Temperate Ecosystems with Seasonal Programming

VOLUME THREE:

D. Natural Arctic Ecosystems with Ice Stress
E. Emerging New Systems Associated with Man
F. Migrating Subsystems

VOLUME FOUR:

Bibliography and Place Index

INTRODUCTION

The estuaries of the United States have always been a major resource in development of America's economy, culture, and way of life. In the severe first winters in New England the natural storages of food in clams and mussels provided critical foods to the early pilgrim colony. Most of the early pioneer cultures were nurtured by the foods and organized by the transportation pathways provided by the tidewaters. Now in the twentieth century, the spread of urban civilization is including the estuaries, alternating cities with wilderness areas in new designs for the planet earth. The new patterns involve wastes, dredging, and industrial uses of the bays which are changing nature so fast that our comprehension is badly lagging in spite of accelerating efforts at scientific studies of estuarine science. Thus in 1968 the Congress of the United States has called for summaries of the status of knowledge of the estuaries pertinent to the planning of management and further study.

The Need for Organizing Knowledge of Estuaries by Type

Following many years of studies of the coastal seas by universities, state government organizations and federal laboratories, the information dispersed in papers, books, reports, and documents is now vast, much of it in local sources outside the mainstream of national consideration and planning. Without some new ways of organizing our knowledge and plans, no individuals can any longer encompass the knowledge pertinent to management of the resources of a single state. Discoveries of relationships in estuaries on the Pacific coast may be the answer to problems developing on the Atlantic coast and vice versa. Inadequate communication results in part from the difficulty of recognizing common features of coastal systems that seem to be different. Some means is needed for organizing the knowledge according to a natural classification of estuaries, one that groups together estuaries with similar responses to disturbance, planning, or management. In recent efforts to describe the estuaries of America, 893 groups of estuaries have been listed. This is too many to consider individually as if they were separate phenomena. Although each system has some properties unique and different, many have common similarities in their basic processes, which allow them to be grouped into types. Whereas studies of single species, single chemical processes, single geological features and single processes of a physical nature have been useful and often rigorous, the behavior of an estuary depends on the total interaction of all the chemical cycles, water circulations, and species behaviors. It is the whole system phenomena that state departments responsible for estuarine resources must consider. Perhaps it is in the systems study of the overall performance that there is hope for prediction and management. The developing science of Ecology is the study of ecological systems (ecosystems) such as forests, lakes, and estuaries, and it is the realm of this science to provide natural ways to group the systems.

Man, A Component in Nature

In the ecological approach to environmental systems man's role is considered as an integral part of nature. An ecological system has inputs and outputs. It processes materials and energies within organizational patterns of water current, chemical processes, living components, and man's uses and wastes. Whether the system is a tiny balanced aquarium or the huge biosphere of the whole surface of the earth, all the users and processors of materials and energy are part. In the same sense urban man is now becoming a part of the coastal systems, often dominating the chemical processes as well as the fishes and microscopic plankton. Where the effective organization of processes breaks down, it may be man who reaps disastrous results. Any classification of estuarine systems must include ancient types that preceded man and that remain in wilderness areas as well as new patterns associated with estuaries newly disturbed by man. Part I presents 48 ecosystem types as a beginning. Others will probably be added as our knowledge progresses.

Estuary or Coastal System?

In one sense, the word estuary may mean partially enclosed bodies of marine water such as lagoons, river mouths, and bays. The problems in management of our coastal seas and seacoasts, however, include the beaches, the intertidal rocks, mud flats, the coastal waters among island archipelagos, zones of the open sea waters along open shorelines, and other configurations which might not fit under the word estuary. America's need and the mission called for by Congress is clearly to organize our knowledge of all the ecological systems of the coast. Thus for this effort we deal with all the coastal systems where man's culture is or soon will be interacting with the sea. Usually, large estuarine bodies of water contain more than one ecological system or subsystem. It is the ecosystems rather than the estuarine water bodies that are discussed and classified here.

Pollution and other Disturbances by Man

The influences of man are presented in our report in two ways. If the influence by man is not sufficiently large to distort the formerly natural ecological system into an unrecognizable structure and type, the disturbance factor is described and documented by the author reporting the story on that type of ecological system. If the energy sources or stresses involved with man's special influence are so large as to predominate and in effect create a new type of system, this influence is recognized as one of the emerging new types of ecological systems self-designing its relationship to man. These are found in the final group of systems (E).

Organization of the Report

Efforts have been made before to classify estuaries according to ecological principles and in Part I we build our classification on these earlier beginnings, although we broaden the basis using theories of energy control. For a classification to be useful, it must serve to condense knowledge, to generalize, to aid teaching, to simplify planning for management, and lead to progress. It should not deal with only one geological structure, water flow, organism, etc. Once recognized, however, the types of systems may be mapped according to the distribution of indicator organisms such as the foraminifera, as described by Nichols in Part II. The presence of small skeletal-bearing organisms allows cores of sediment to be studied as a record of former systems. For each type of system that we define here, there follows a chapter summarizing its usual structures and processes. Bibliographic references are cited by system. Some are also cited by state.

If estuaries have sometimes been handled in the past without adequate thought for overall system properties, a classification may help to guide future programs into a more rational organization. If the populations and properties of a coastal ecological system require management of the whole, a recognition of the main types of systems should help to eliminate efforts to deal one at a time with one species, one problem, or one component locality. The main function of our report is to identify, characterize, and document some examples of each important type of coastal ecosystem. Remarks pertaining to individual states in Part III suggest the distribution of system types and their manner of application. However, there remains the need for separate studies in each state to map and designate types in each estuary.

Part IV has the report's overall recommendations concerning further study and management of the coastal ecosystems.

Part V has chapters on each type of system. Knowledge about an ecological system can be introduced under 5 headings:

1. Summary of Components by Name, Mass, Number
2. Vertical Patterns
3. Horizontal Patterns
4. Flow Pathways
5. Temporal Patterns

However styles and order of presentation of material by the various authors vary. Where a specialist was not available to supply a chapter, the editors have provided a substitution.

Part VI is the bibliography arranged alphabetically with pertinent state or locality indicated. The letter code (the same as that used in the table of contents) identifies references pertinent to a system type. Included separately is a bibliography of estuarine bibliographies.

Systems Analysis and Simulation

Although estuarine science is only now entering the simulation phase, data on components and structure (items 1-4 above) provide means for simulating with computer programs that give the temporal consequence (item 5) of the structural patterns of species and chemical concentrations. If the computer simulation produces a temporal pattern in the system's behavior that matches the observed pattern with time, then one has some evidence that the component theories of the behavioral interactions of the parts built into the program are applicable to the real one with some utility for prediction, for experimental testing, and for incorporation into a harmonious pattern of man's newest civilization. Its use in systems modeling is one reason for this effort to reorganize estuarine knowledge, recognizing a relatively few kinds of coastal systems, each of which can be simulated. With realistic simulation, rapid testing of expensive propositions with computer models may be arranged before tampering with the great estuaries themselves.

ACKNOWLEDGMENT

The Department of Zoology, the Department of Environmental Science and Engineering, the Marine Science Curriculum of the University of North Carolina, and the Marine Science Institute of the University of Texas collaborated with local support.

We are grateful to the many scientists and resource managers in the coastal states who responded to our mission, participating in the discussions of estuarine typing that were held in each state in the autumn of 1968. Mr. David Howells of N. C. arranged state interviews through the Water Resources Institutes. Assistants on the project were: Kirsten Canoy, Joyce Shields, Ann Rogers, Henry N. McKellar, Richard Chalcraft, Kenneth Perez, David Bridges, Frances Dickens, G. M. McClain, Glenda Sommers, D. W. Stanley, D. J. Yates, and Jesse Edwards, Jr.

Part I

A FUNCTIONAL CLASSIFICATION OF THE COASTAL SYSTEMS OF THE UNITED STATES

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INTRODUCTION

It is an intuitive belief among marine scientists that each estuary and coastal system is unique and different, probably because there are so many possible combinations of important factors of geology, climate, tide and history that identical combinations are improbable. However, similarities do exist even among estuaries widely separated on opposite coasts of the United States, so that it may be possible to classify the hundreds of estuaries into a relatively few types. We propose herewith a classification of the coastal systems of the United States according to the most prominent processes dominating the functional activity of the system. To clarify concepts and terminology we will first describe briefly the characteristics of any ecological system. After reviewing some previous efforts at estuarine classification, we will present the proposed theory of classification based on dominant energy flows. It is a basis that includes biological, geological, chemical and physical classification factors, energy being a common denominator.

An ecological system consists of populations of organisms, flows of water, invisible pathways of cycling chemical elements and various organizational mechanisms which cause the parts to be inter-related. A bed of underwater eelgrass, with producing plants, micro-organisms and animals, is an ecological system. So is a bay in which water circulates and indigenous microscopic planktonic organisms develop, exchanging minerals from the bottom to the top in continual flows. Wherever there are special conditions, the marvelous self-designing property of ecological systems produces special adaptations, characteristic species of clams and fish and properties that are uniquely characteristic of that special condition. In the tropics there are coral reefs and in the Arctic there are systems that are adapted to ice and icy waters. Where the conditions pulse, the patterns and programs of the ecological system may pulse in response. Because conditions are never exactly the same, the systems which develop are all unique, but there are similarities that may form the basis for grouping and classification.

Classification is necessary in the affairs of man, for where information is diverse and extensive the limits of the human mind require categories and simplified summaries for comprehension. The knowledge and publications on estuariesare so vast that clear perspectives are sometimes drowned in data. Patterns studied in one estuary may not be recognized as similar and recurring in another. As the problems with preservation and development of estuaries become acute with expanding populations, there is increasing need for a classification that has meaning for planning and management. For the summaries of the state of knowledge on estuaries requested by the Congress of the United States for 1968, a classification according to the principles of ecology may increase comprehension and simplify future planning.

CHARACTERISTICS OF ECOLOGICAL SYSTEMS

The general characteristics of an ecological system may be illustrated by the diagrams in Figs. 1-5. The following is a theoretical discussion of the relationships of various system components.

Visual Summary Diagram

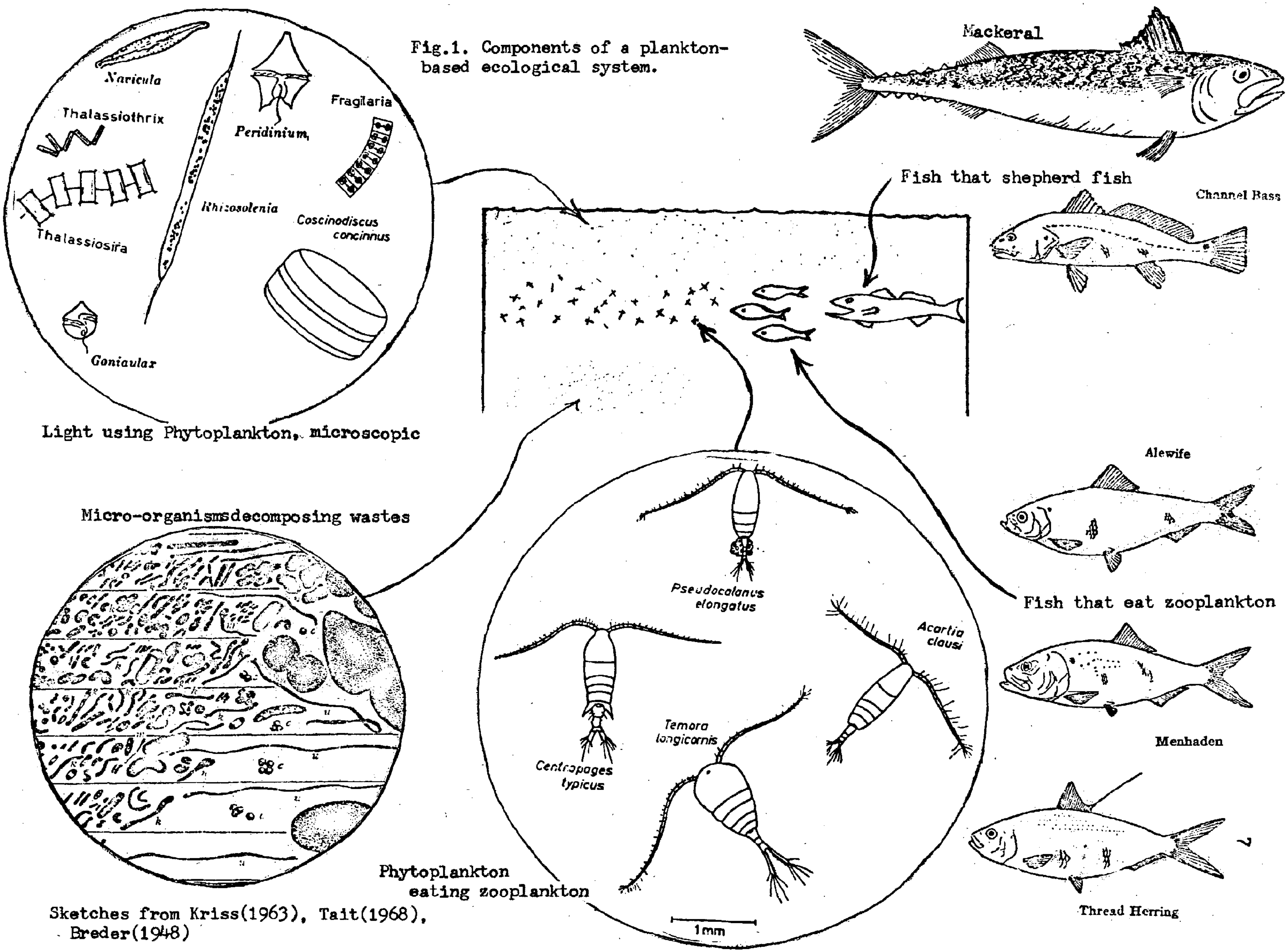
Perhaps the first step in summarizing an ecological system is to present a visual inventory of the main components of a system. Thus Fig. 1 is a diagram that gives a visual summary of principal species of animals and plants that constitute the main control structures of the flows and processes of a plankton system in a deep bay. In such a diagram, one simplifies by including those species and non-living structures that are most dominant (i.e., most important by weight per area). One includes principal swimming species and principal bottom consumers. If data are available one includes a graph on the average masses of principal components. Such inventory of components alone gives little idea of the way the system works, but the presence of characteristic species with known special adaptations suggests the nature of the system. Thus, species are known that are characteristic of plankton life, bottom life, low salinities, wide ranges of stress, low temperature, etc.

The public has often been misled by concentrating their interest on large visible organisms, whereas the important issues of yield, stability and water quality are more concerned with maintaining an effective flow of energy and mineral cycles. The populations of larger animals tend to be switch feeders taking some of many inputs, especially any flow that becomes excessive, and serving by their omnivorous role to even out the total energy flow web while supporting themselves. Because of the phenomenon of converging food pathways into the larger animals, these animals may smooth out small local variations and thus are sometimes useful as indices to classifications of system types where overall management planning may be involved.

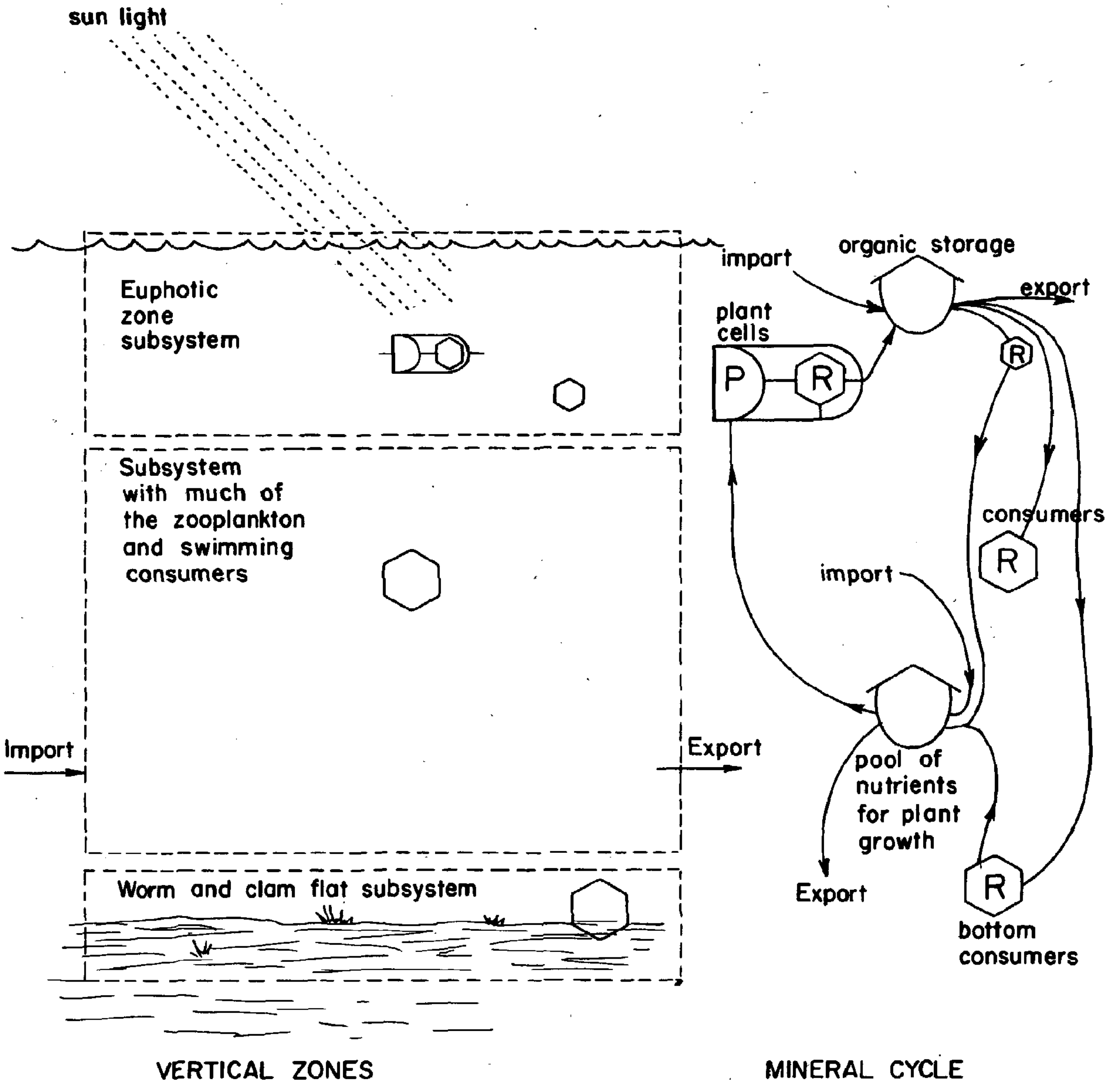
Vertical Patterns

In vertical aspect (Fig. 2) the ecosystem can be divided into main zones relative to light energy that enters the system from above. The upper zone, where photosynthesis of microscopic plankton algae occurs, is marked with a P for primary productive photosynthesis (a process that uses fertilizer, carbon dioxide and mineral elements to make organic food for the rest of the food chains and at the same time releases oxygen).

Fig.1. Components of a plankton-based ecological system.


Navicula
Thalassiothrix
Thalassiosira
Rhizosolenia
Peridinium
Fragilaria
Coscinodiscus concinnus
Goniaulax
Light using Phytoplankton, microscopic
Micro-organismsdecomposing wastes
Mackeral
Fish that shepherd fish
Channel Bass
Alewife
Fish that eat zooplankton
Menhaden
Thread Herring
Pseudocalanus elongatus
Acartia clausi
Temora longicornis
Centropages typicus
1mm
Phytoplankton eating zooplankton

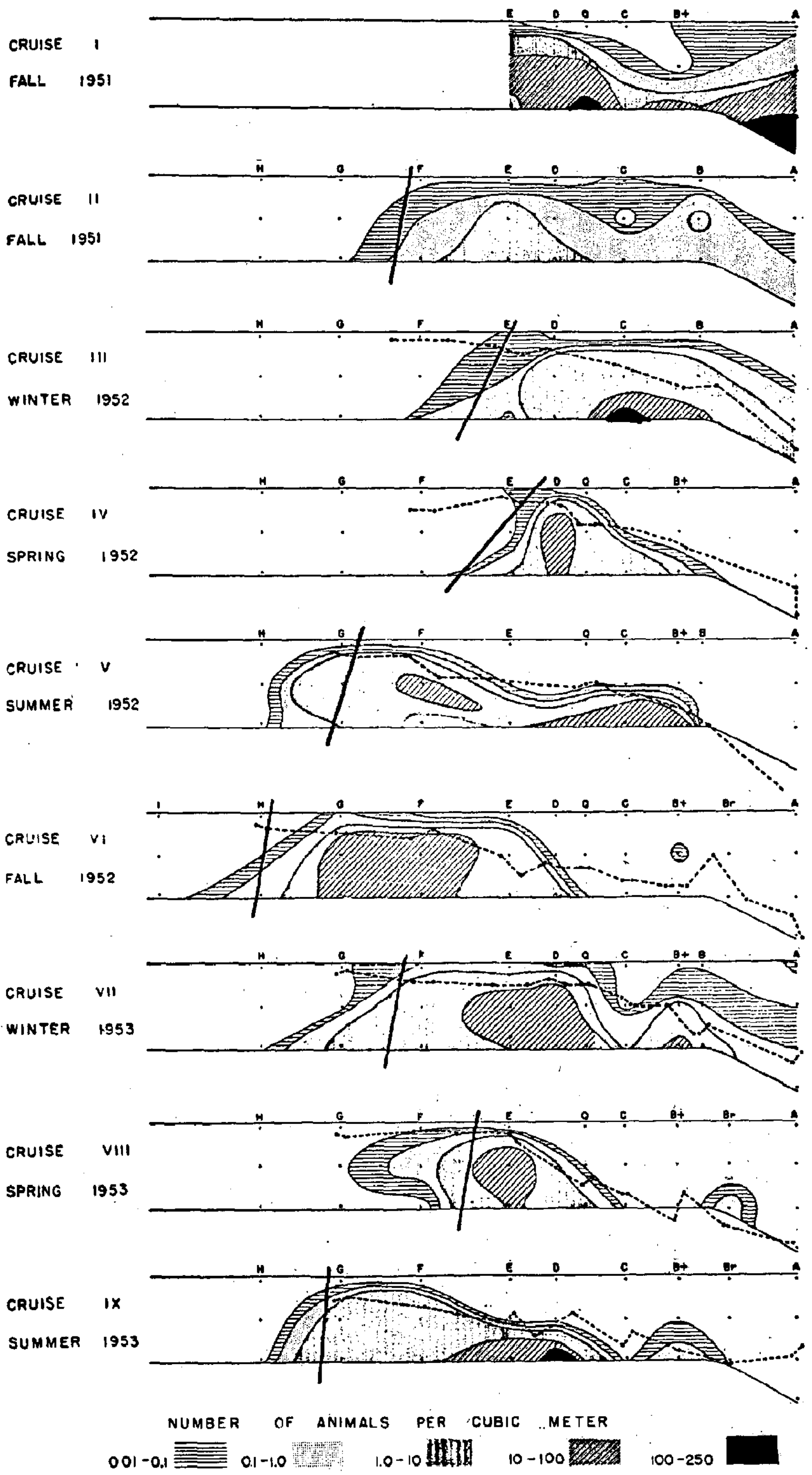
Sketches from Kriss(1963), Tait(1968), Breder(1948)


sun light
Euphotic zone subsystem
Subsystem with much of the zooplankton and swimming consumers
Worm and clam flat subsystem
Import
Export
import
organic storage
export
plant cells
P
R
R
consumers
R
import
pool of nutrients for plant growth
Export
R
bottom consumers

VERTICAL ZONES

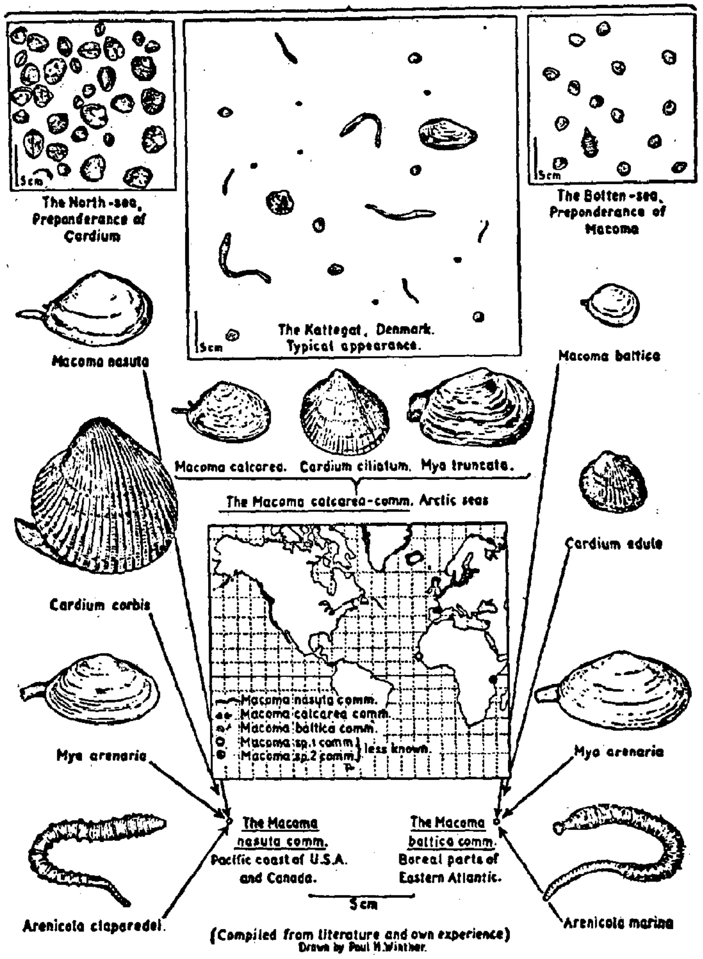
MINERAL CYCLE

Fig. 2A. Vertical zones in an estuarine ecosystem showing photosynthetic production above and most of the respiratory consumption (R) below, the mineral cycle circulating plant nutrients upward and organic matter for food downward with the action of stirring waters and swimming animals.



The vertical distribution of *Neomysis americana* along the axis of the estuary. The dashed line is the depth of the critical light intensity. The nearly vertical straight line is the 4‰ isohaline.

Fig 2B. Example of a population of intermediate consumers(Mysid shrimps) retaining position in an estuary as waters flow in and out. Delaware River Estuary(Hulburt, 1957)


The North-sea, Preponderance of Cardium
5cm
The Kattegat, Denmark. Typical appearance.
5cm
The Botten-sea, Preponderance of Macoma
5cm
Macoma nasuta
Macoma baltica
Macoma calcarea. Cardium ciliatum. Mya truncata.
The Macoma calcarea-comm. Arctic seas
Cardium corbis
Cardium edule
Macoma nasuta comm.
Macoma calcarea comm.
Macoma baltica comm.
Macoma sp.1 comm.
Macoma sp.2 comm.
less known.
Mya arenaria
Mya arenaria
The Macoma nasuta comm.
Pacific coast of U.S.A. and Canada.
The Macoma baltica comm.
Boreal parts of Eastern Atlantic.
5cm
Arenicola claparedei.
Arenicola marina
(Compiled from literature and own experience)
Drawn by Poul H. Winther.

—Diagram showing the parallelism between the Arctic, the boreal, and the Northeast Pacific Macoma *communities*
Drawn by Poul H. Winther; G. Thorson dir., Orig.

Fig. 2c. Substitution of species in parallel communities (Thorson, 1957).

Deeper down in the shade, the consumption of organic food by animals, microorganisms and plants (termed respiration) is exceeding photosynthesis, and the overall process reaction is the reverse. When organic food is consumed, oxygen is used and minerals and carbon dioxide are released to the water again. An effective ecosystem circulates the products of one zone or layer as inputs to the processes of the other either by using natural circulation processes of the water motions or by supporting animal, plant and microbiological organisms that accomplish the same result through expenditures of work in such living processes as swimming, pumping streams of water or concentrating chemicals. All contributing structures, such as the populations of living organisms participating in the system, have to be maintained by expenditure of work. The respiratory consumption of food and oxygen measures the magnitudes of work involved in self maintenance.

The tasks of work are divided up among specialists. Whereas some organisms are specialized by their biological adaptations to start microscopic plant food through the food chains, others are adapted to process foods accumulated by small animal plankton (water flea size) and still others (e.g., larger fishes) are adapted to cover large areas and perform distributional roles in consumption of foods and cycling of nutrients. The specialized tasks in the ecological systems are performed by different species, and the significance of variety in living organisms includes the separation and specialization of functions of particular adaptive value. In stratified systems where normal vertical circulation is limited by the stability of the two-layered stratification, the mechanism of vertical migrations by organisms is an adaptation for vertical circulation of food, minerals and work.

Although these summarizing statements do not begin to convey the complexity of reactions of the many organisms participating in the living control processes, they suggest the contributions to the system as well as the self-serving roles of their activities. The presence of a species is tied not only to its own abilities to utilize the available inputs and outputs, but also to the presence of a life support system that provides the correct combinations. Both the components and the overall flows of energy must be maintained without shortages and excesses. If this balance of cycling fails, the system is less effective in processing food energies and is subject to replacement either as a whole or by substitution of parts.

Horizontal Patterns

The main energy flows in estuarine systems have lateral dimensions in map view from above (as in Fig. 3), especially where there are strong water currents that organize the populations into gyrals and integrate food and consumers in ways that are regenerating and continuing. The horizontal patterns help show the organization of the pathways between the plants that must be spread out to catch the sunlight and the centers of consumption (the animal cities) where the regeneration of plant minerals occurs in concentrated centers of activity. In urban culture transportation does this, but

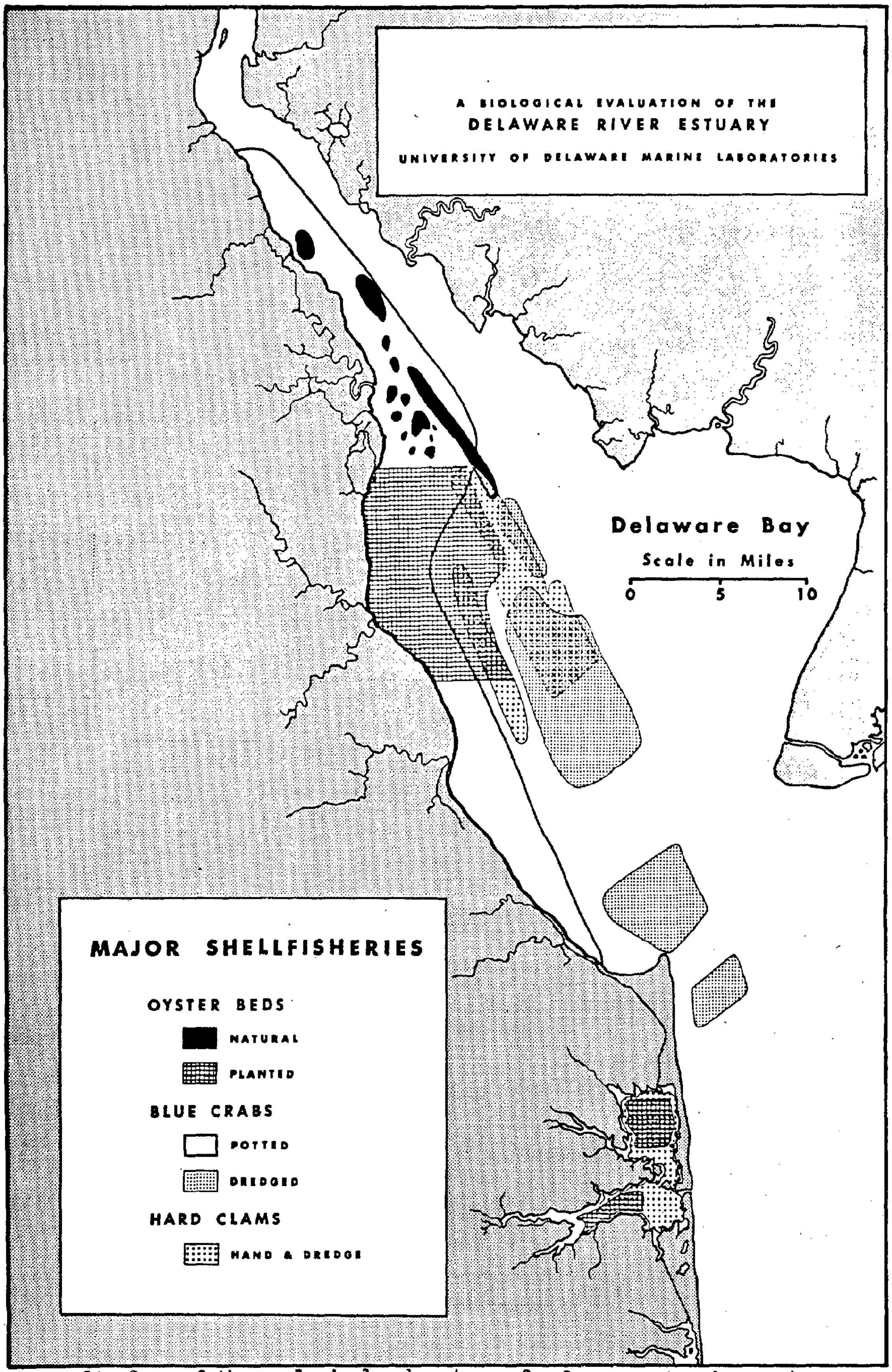
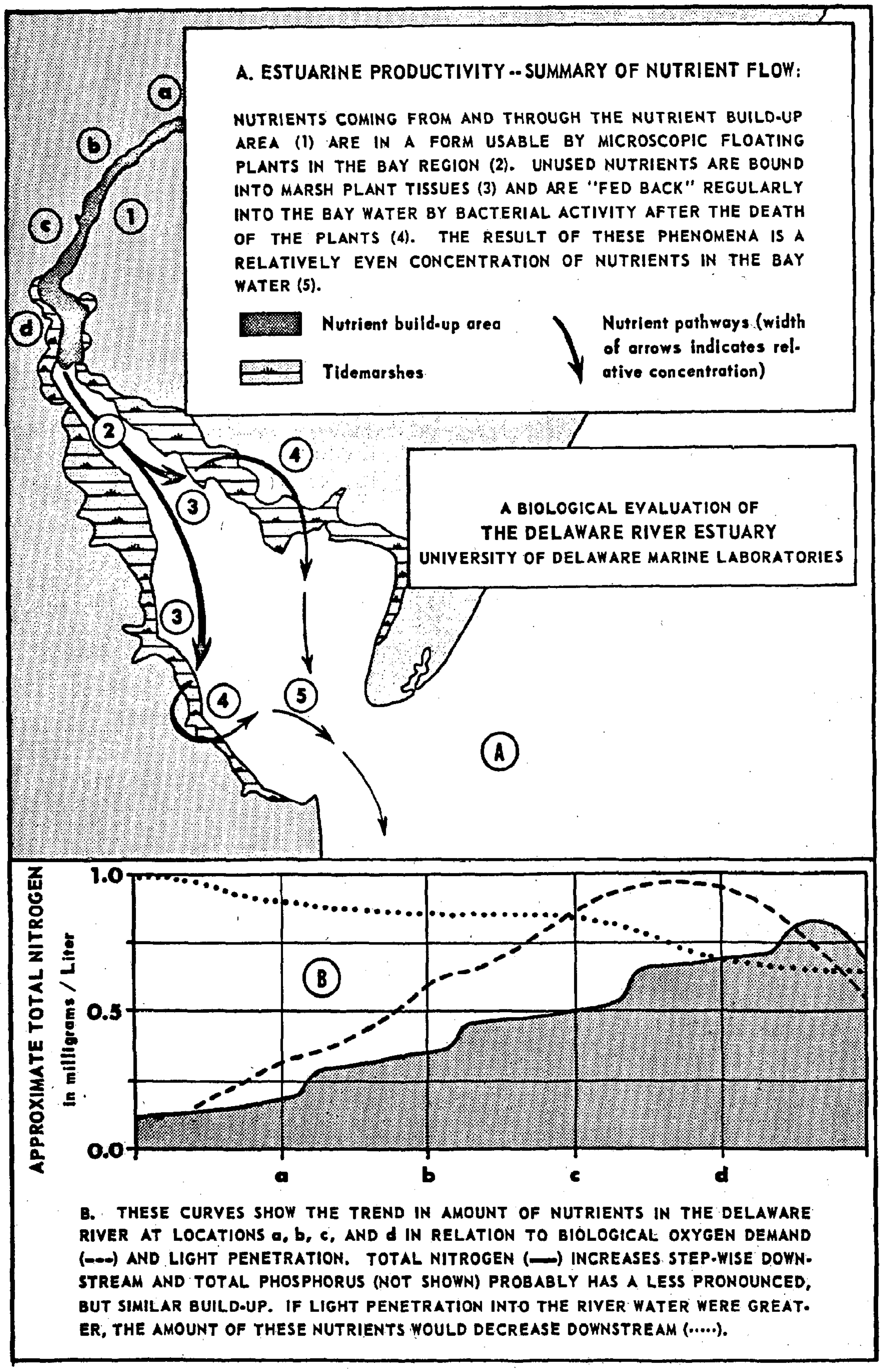

A BIOLOGICAL EVALUATION OF THE
DELAWARE RIVER ESTUARY
UNIVERSITY OF DELAWARE MARINE LABORATORIES
Delaware Bay
Scale in Miles
0
5
10
MAJOR SHELLFISHERIES
OYSTER BEDS
NATURAL
PLANTED
BLUE CRABS
POTTED
DREDGED
HARD CLAMS
HAND & DREDGE

Fig. 3A. Some of the ecological subsystems of a larger estuarine system, Blue crabs participate in bottom subsystem and the main plankton system above (Shuster, 1959).



A. ESTUARINE PRODUCTIVITY -- SUMMARY OF NUTRIENT FLOW:

NUTRIENTS COMING FROM AND THROUGH THE NUTRIENT BUILD-UP AREA (1) ARE IN A FORM USABLE BY MICROSCOPIC FLOATING PLANTS IN THE BAY REGION (2). UNUSED NUTRIENTS ARE BOUND INTO MARSH PLANT TISSUES (3) AND ARE "FED BACK" REGULARLY INTO THE BAY WATER BY BACTERIAL ACTIVITY AFTER THE DEATH OF THE PLANTS (4). THE RESULT OF THESE PHENOMENA IS A RELATIVELY EVEN CONCENTRATION OF NUTRIENTS IN THE BAY WATER (5).

Nutrient build-up area
Tidemarshes
Nutrient pathways (width of arrows indicates relative concentration)
A BIOLOGICAL EVALUATION OF
THE DELAWARE RIVER ESTUARY
UNIVERSITY OF DELAWARE MARINE LABORATORIES
a
b
c
d
1
2
3
3
4
4
5
A
B
APPROXIMATE TOTAL NITROGEN
in milligrams / Liter
1.0
0.5
0.0
a
b
c
d

B. THESE CURVES SHOW THE TREND IN AMOUNT OF NUTRIENTS IN THE DELAWARE RIVER AT LOCATIONS a, b, c, AND d IN RELATION TO BIOLOGICAL OXYGEN DEMAND (---) AND LIGHT PENETRATION. TOTAL NITROGEN (—) INCREASES STEP-WISE DOWNSTREAM AND TOTAL PHOSPHORUS (NOT SHOWN) PROBABLY HAS A LESS PRONOUNCED, BUT SIMILAR BUILD-UP. IF LIGHT PENETRATION INTO THE RIVER WATER WERE GREATER, THE AMOUNT OF THESE NUTRIENTS WOULD DECREASE DOWNSTREAM (·····).

Fig. 3B. Other subsystems in the Delaware Estuary system. The dark area is the oligohaline ecosystem (Shuster, 1959).

in aquatic coastal systems it is often the wind and tidal current patterns that control the pattern of horizontal organization. By circulating mechanisms or by back and forth shifts of waters, the production process is coupled to the consumption process to give full function.

Pathway Patterns

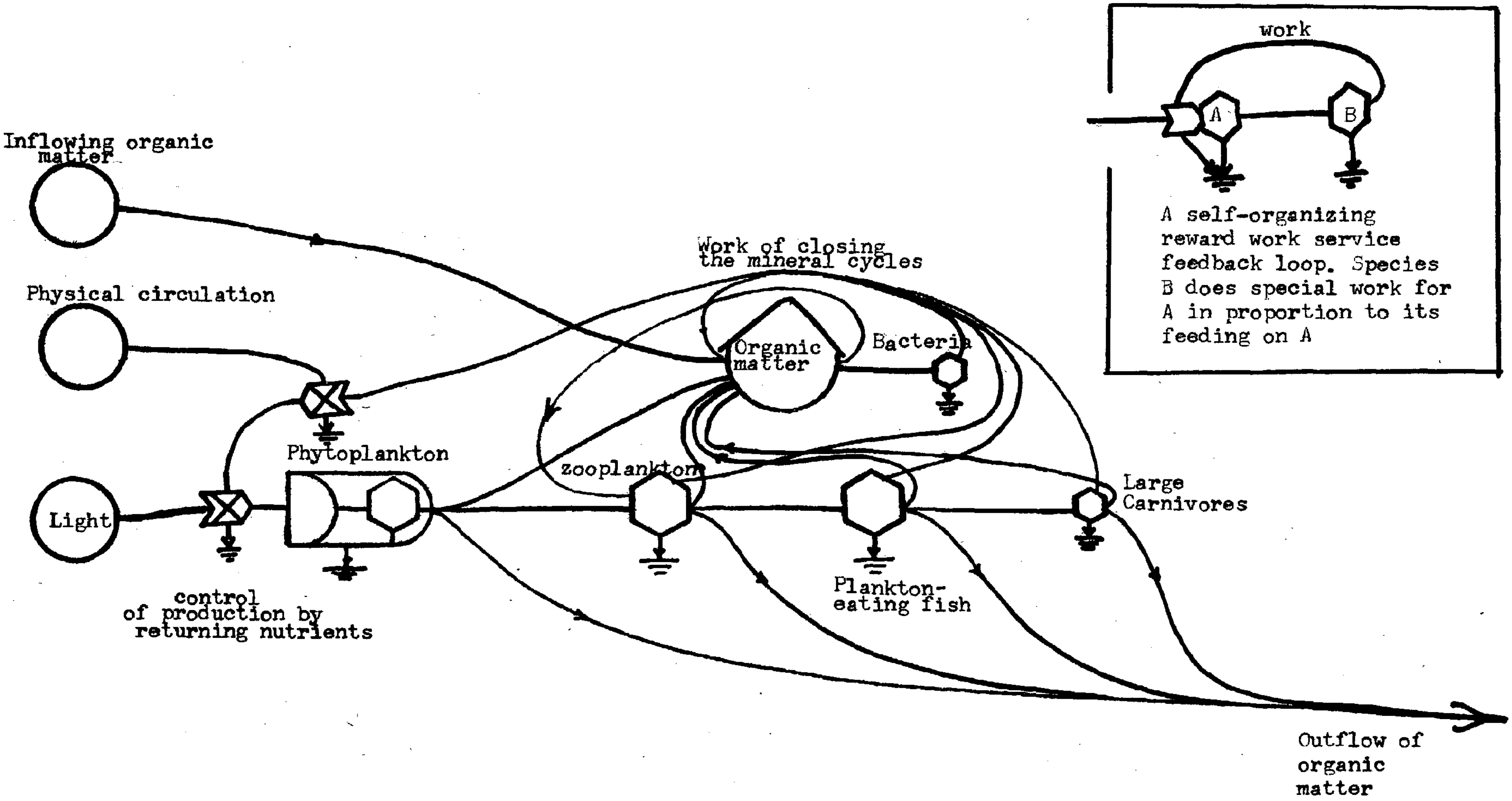
The pathways for processing of food, minerals and work are drawn using pathway diagrams (Fig. 4). Here, it is the inputs and outputs that are important rather than the positions of the organisms in space. New work diagrams help to identify occupation roles of the principal species and to characterize the ways that a system is special in its fine tuning of performances in the work network. The energy flow diagram is one of the ways for showing the pathways for food, work, interactions of species, chemical cycles and the actions of man. In the general energy diagram in Fig. 4, are indicated several kinds of energy sources by which potential energy capable of driving work processes enters from outside. In estuaries, the sun operating the plant production processes and the organic fuels entering with rivers are most important. Fig. 4 also indicates the energy drains in a system. As required by the laws of energetics, some potential energy disperses as unavailable heat at every step and this is indicated by the symbol resembling an arrow into the ground. Also leaving the system as energy drains are exports of potential energy as when fish are harvested, when they migrate out of the estuary or when, during decomposition, some organic matter is buried into the sediment deeply enough to be permanently out of the chemical processes of the estuary.

A stress on an estuary is a process that drains energy. It can be either directly as with fish harvest, or indirectly as by diversion of energy sources that the bay would have received (e.g., when turbidity shades out the light or when some property injurious to life is added so that energies of surviving organisms are diverted into special work of repair replacement or into programming of special behavior required to adapt to the special property). Thus, for example, adding salty brines to an estuary raises the energy cost of operating kidneys and maintaining a proper blood chemistry so that only a few special organisms with the equipment for this can adapt.

Thus the energy diagram in Fig. 4 helps to identify the special energy inputs or stresses characteristic of an estuarine system while showing the main uses of this energy within the network of living and nonliving components of the whole system.

Temporal Patterns

An ecological system also has its temporal characteristics according to the course of the day, the tidal cycle and the season. Since the combinations


work
A
B
Inflowing organic matter
Physical circulation
Light
control of production by returning nutrients
Phytoplankton
zooplankton
Organic matter
Bacteria
Work of closing the mineral cycles
Plankton-eating fish
Large Carnivores
Outflow of organic matter

A self-organizing reward work service feedback loop. Species B does special work for A in proportion to its feeding on A

Fig. 4. Simplified diagram of the flow of potential energy in an ecological system ultimately emerging as dispersed heat or export of potential energy. Species are grouped according to similar food sources. For symbols see Fig. 7.

of energy inflows and stresses in a given system are usually unique the adaptations of the organisms also form unique combinations that provide for programming of the biological and chemical processes so as to fit the energy timing. For example, the migration of many fishes and shrimp is programmed so that the demands on the systems energy budget coincide with the seasonal pulse of available energy. The adaptation serves a dual purpose: it gives the species the best possible competitive position relative to alternative species that might occupy that role and it provides a hand-in-glove fit of the food chains to energy budgets so that the system of processing as a whole is regulated, stabilized and increased in overall effectiveness in its competition. In describing any estuarine ecosystem, some graphs of pattern with time are essential, showing the timing of special energy sources of light and river flows, stresses such as severe temperature change and pollution, and the programs of adaptation such as reproduction of organisms or blooms during periods of maximum growth. Figure 5 illustrates temporal patterns of energy source, energy stress and internal programming.

HISTORICAL ROOTS OF ECOSYSTEM CLASSIFICATION

The classification of ecological systems according to overall types was a major objective of the early ecologists and geographers starting in the last century. Under the phrases "plant formation" and "vegetation type" characteristic plant associations were named on land to classify ecological systems relating vegetation to causative climatic factors. Classification of climates was related to the vegetation types as in a treatise by Köppen (1931) although definitions were in terms of rainfall, temperature and other meterological properties. Soils were classified in a similar way. Sometimes the soil type was related to vegetation type and a soil map made by mapping the vegetation. Since soil of natural systems was developed by the ecological system and its pattern of productivity and mineral cycles, soil is really a subsystem of the vegetation and its processes. In forests and grasslands animals are small in relative weight but serve important control functions. The word "biome" was generated to describe the large overall classifications of systems recognizing the moving animal populations as a necessary part in addition to the vegetation and soils. The tundra, coniferous forest, the rain forest, etc. are biomes found the world over in characteristic climatic zones. The disturbed systems of the land were usually related to agricultural use so that by typing the soil the existence of new types of man-made systems were implied. Agricultural systems have also been recognized, the soil subsystem being an important part. The mapping and typing of systems of the land has been a major part of resources use and management. The advanced state of land classifications is represented by Shelford's (1963) summary of land ecosystems of North America, by Kelloggs(1967) classification of soil types, and Lieth and Walter's (1967) Atlas of climatic types in relationship to vegetation.

In lakes, typing was related to the main features of oxygen, plankton, and main dissolved chemicals, which were often dependent on the geology of the lake region and the geomorphology of the lake-forming processes. The lake

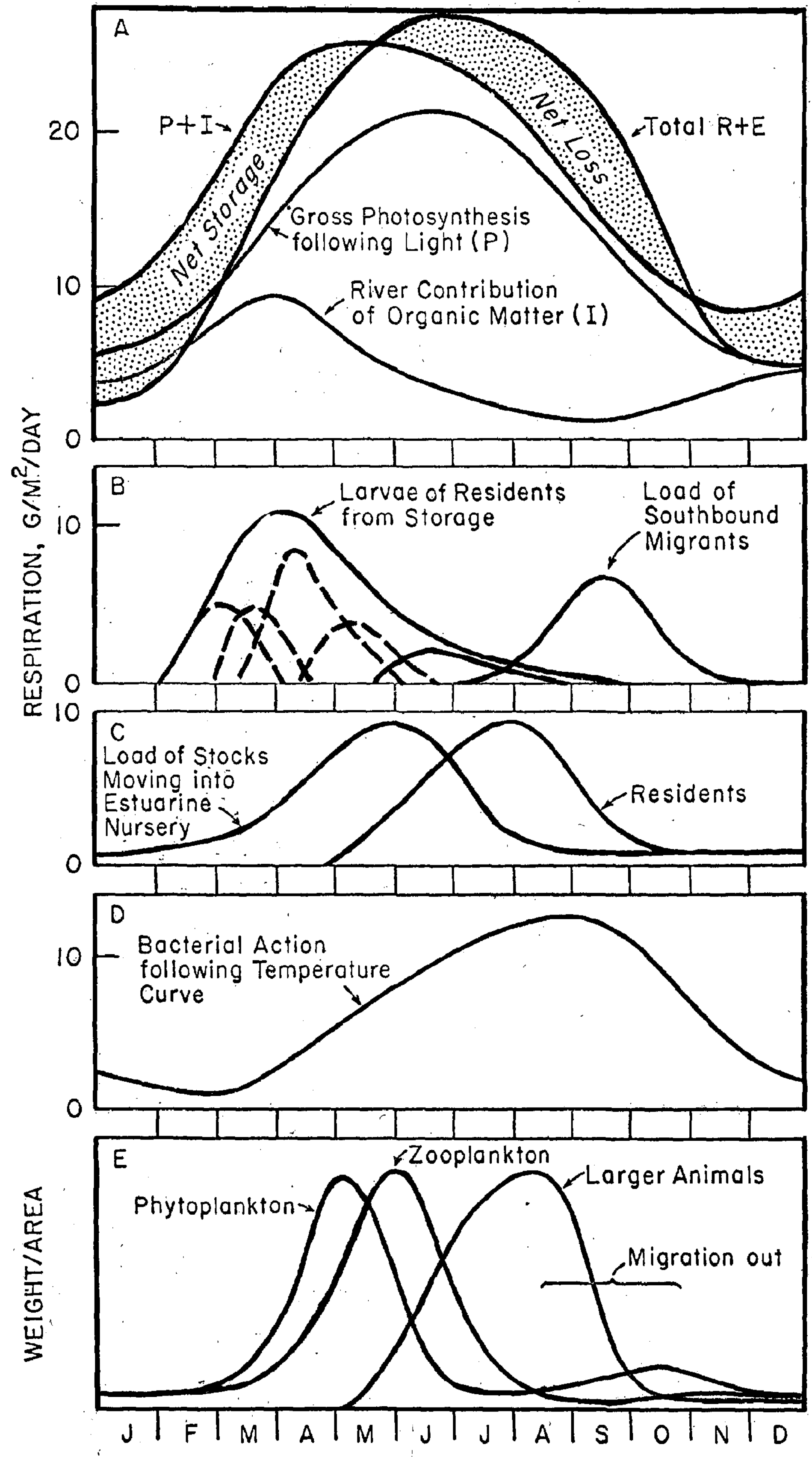


Fig. 5. Diagrams representing hypotheses of complementary coupling of energy loads and energy sources in the course of a year in a temperate regime with spring river runoff.

was readily recognizable as a single system of circulating minerals and media binding the plankton and bottom animals into a single interdependant network (Nauman 1932). Lake typology methods were extensively applied to Northern Europe. The treatises on Limnology by Hutchinson (1957, 1967) provide general summaries. A detailed classification of American lakes as systems has not been made, but Frey's Limnology of North America (1963) provides a summary of the limnological studies by state.

Streams reflect the characteristics of the drainage basins, deriving their solution properties from the rocks, ground waters and land systems drainage. Streams were typed by chemical content and related to regional land type. The water supply papers of the U. S. Geological Survey extend principles set forth in Clarke's (1924) Data of Geochemistry. More recently states have attempted management classifications on the basis of waste present and disturbance.

In lakes and streams, boundaries of the system are usually distinct at the contact with land. Identifying the boundaries of systems was not the difficult problem it is in the sea. In the sea, with its interconnecting water exchanges forming one giant oceanic system, typing of subsystems was much more difficult because the boundaries of component systems were not clear, the dominant chemical and biological processes were mainly invisible and the areas so vast. Since the sea animals do much of the work that plants do on land and the biome name seemed appropriate, Petersen (1913) in Europe and Shelford (1913) and Shelford and Towler (1925), using data from the sounds of Washington in the U. S., attempted to extend the methods of terrestrial biome classification to estuaries. Examining the bottom animals and plants, they named the systems according to the one or two most abundant visible large animal species there. This now seems a reasonable approach where the bottom system is the focus of interest or is a characteristic part of the estuarine energy flows and mineral cycles (e.g., with shallow eelgrass). Even when the estuary is dominated by plankton processes, the bottom animals may characterize the total estuarine process if diversities are small and adaptations of plankton and bottom animals are both determined by similar factors such as salinity stress. Thus Parker (1959), using molluscs, and Phleger (1960a), using foraminifera, may be cited among those who followed Shelford in the use of bottom animals to characterize associations of estuaries with some success. These classifications allowed sediments in the geological record to be studied in terms of the ecological system at the time of their formation, a field called paleoecology.

In high salinities and less stressed environments, Shelford's classification of bottom associations had less significance as a measure of the estuarine systems in which the association occurred. In the higher salinities, as in the open sea, there is a finely tuned division of labor among many slightly different specialized species. Each species may form animal cities of a few acres participating as a subsystem, filtering the water that passes as it circulates over much larger areas, becoming a giant pool of nutrients and productive plankton. No one bottom association is dominating the processes of the overall circulating energy and mineral cycling system. By moving, the plankton would have more tendency to integrate the patterns over the larger area except that they are so small that they fluctuate and change with small temporal transients so that no one collection can represent overall effects. The small plankton in the big systems also differentiates into patches, each with different species predominating. Shelford's bottom classification in the more stable waters of larger dimension does not cover enough of the subsystems to represent the main functional processes, although it may be valid for the subsystem types of the bottom.

As the size and circulation energy of a marine system gets larger, the size of the component functions may increase. A small sheltered basin may have ten species of bottom animals dispersed in heterogeneous groups so that a few dredge samples may give an adequate statistical representation of the whole system. In larger systems, however, such as the coastal continental shelves, the bottom is differentiated into many subsystems each dominated by one or two species locally predominating in vast masses over many acres; but no one sub-system really predominates when one considers the overall large areas over which water slowly circulates in large gyrals. The sea systems of the open continental shelf allow the plankton to maintain some continuing patterns as they pass from one bottom subsystem type to another. In such large systems, classification of bottom subsystems species would have meaning only if it were done over the whole area of the water gyral and the frequency of sub-system types enumerated. We may cite works of Zenkevich (1963) among those attempting to characterize the open shelves and deeper bottoms. Whereas an acre of land has much of its main energy flow and mineral cycle self-contained, an acre of marine bottom in deeper water is only a contributor to the larger energy and mineral cycling systems of the circulating water above. Shelford's effort to extend the biome concept to deeper marine waters did not recognize the nature and location of the main organizational energy flows in the water above or the mechanisms for holding ecosystems organized in moving water.

Efforts to define biomes of the estuaries were more successful where organisms were specialized in adapting to particular factor-dominated situations. Thus the Stephensons (1949) and Doty (1957) characterized intertidal zonations of algae, Shelford (1930) the barnacle zones, where adaptations to fluctuating water levels produce similar patterns. Pearse (1950) generalized on the beach system of the world. Emery's book (1960) on the sea off southern California considers its subsystems although it stops short of systems analysis.

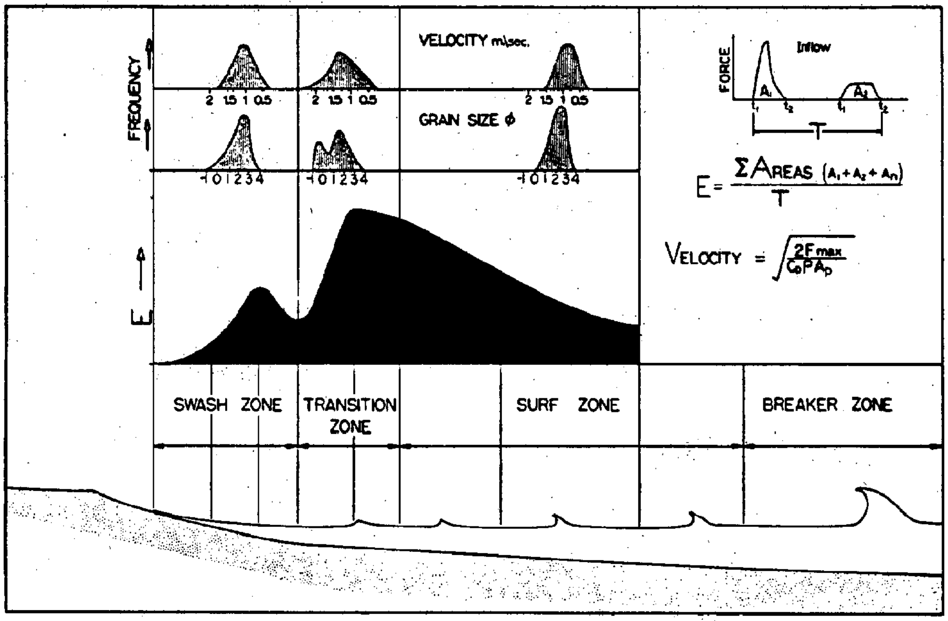
Bullock (1958) shows the physiological temperature-metabolism mechanisms that permit an adapted species to control its metabolism to a level matching the rates of food supply of the niche. From these data we infer that crude adaptation is possible within one species, but finely tuned adaptation is done by substitution of species because of the economy of saving on physiological machinery. Hedgepeth (1957)(chapter 13) reviews early efforts at classification, shows similarity of northern and southern hemisphere associations, reviews efforts to invoke the history of the animals' distributions to explain patterns, and following Louis Hutchins (1947) and others confirms the fact of species substitution with temperature regime. He does not recognize that each species must also find a characteristic energy role for which it is preadapted and attracts a positive feedback. The Treatise on Marine Ecology edited by Hedgepeth (1957) was organized by environmental type but few of the authors considered system requirements (such as mineral cycling performance and feedback reward work) as causal prerequisite for organization of a species into the surviving network (see Fig. 4, inset). Thorson (1957) set forth a parellel communities concept. By recognizing species substitution in roles of specialization, he recognized relatively few types of bottom ecosystems. See, for example, Fig. 2C.

Chapman (1964) in his book on coastal vegetation uses chapter headings: rocky shores, algal vegetation (sections on Laminaria beds and on intertidal brown algae), salt marshes, sand dunes, shingle beaches, and coastal cliff vegetation. By recognizing the basic similarities in vegetation by environment, from world wide examination his presentation defines several of the types used in our classification.

With fewer parameters to consider, geologists, considering the sedimentary bottoms of modern estuaries as a guide to understanding the sedimentary rocks, studied mineral properties and grain sizes of sand, silt and clay. Because high current and wave energies maintain the smaller particles in suspension, the bottoms have grain size and density in proportion to the energies of water motion. An energy classification of sedimentary environments was developed, with beaches and bays being classified appropriately. Efforts to relate animals and plants of these bottoms to the sediments made sense when the common dependence of sediment and plankton feeders on water motion was recognized. The magnitudes of energy flows are clearly a useful basis of coastal classification in these studies and may be cited. Munk and Sargent (1954) determined horsepower per foot of reef at Bikini Atoll as a morphogenetic factor in development of coral reef ecosystems. Sakou (1965) measured energies affecting the morphology of Hawaiian beaches. Schiffman (1965) showed the distribution of breaking wave and current energies on a beach (Fig. 6A). The difficulty with these efforts as a general classification is that only one kind of energy flow was considered. Light energies and organic food flows were omitted. Fig 6B shows the relation of current energy to sediment size and clam density.

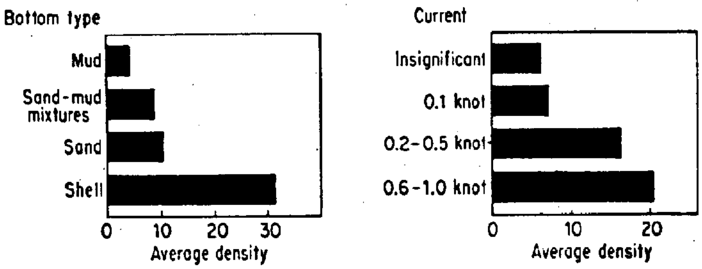
Also geological in origin are the classifications of estuarine landforms according to the processes and types of landforming energy flows. Rise and fall of the land relative to the sea, the previous actions of glaciers and the erosion of rivers provided a classification of the estuarine basins (Johnson, 1919). The accumulated work of prior energy flows in forming estuarine structure was a basis for this classification which may be represented by theories of entropy control by Leopold and Langbein (1964). Whereas geological structures have a major role in controlling the continuing flows of estuarine energy, they are not sufficiently determinative to serve as a classification of the ecological systems in the estuaries. Thus two basins of similar geomorphologic type may be entirely different if the tides or the chemical contents of the rivers differ.

For physical oceanographers studying the water motions in the estuaries, the distribution of salt and density of water was important. Pritchard (1952b) classified estuaries according to salinity patterns and the role of rivers, evaporation, depth and tidal energies in producing estuaries. He found well-mixed river-sea water blends, two-layered estuaries with salt wedge on the bottom, estuaries with salinity higher than the sea because of more evaporation than freshwater inflow and neutral estuaries having no net change in salinity of sea water while in the estuary. This classification by salinity summarizes the interaction in one respect of several kinds of energy drive converging in the estuary, but it does not summarize all pertinent processes affecting


FREQUENCY
VELOCITY m/sec.
2 1.5 1 0.5
GRAN SIZE φ
-1 0 1 2 3 4
E
FORCE
Inflow
A_1
A_2
t_1 t_2
T
$E = \frac{\Sigma \text{Areas } (A_1 + A_2 + A_n)}{T}$
$\text{Velocity} = \sqrt{\frac{2F_{max}}{C_D \rho A_p}}$
SWASH ZONE
TRANSITION ZONE
SURF ZONE
BREAKER ZONE

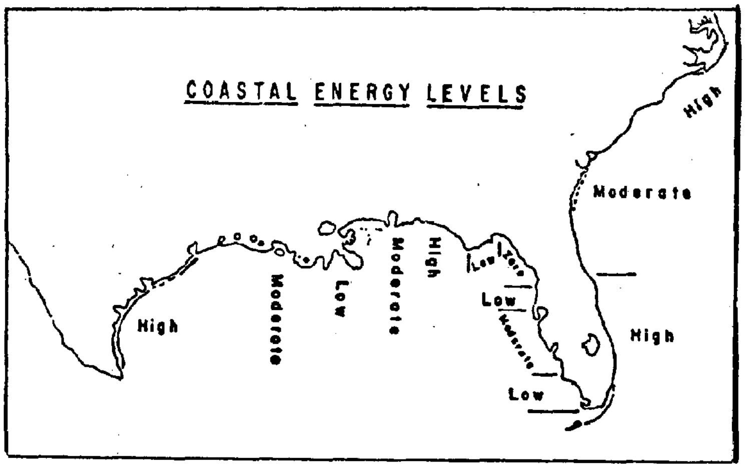
Generalized bottom energy profile.

Fig. 6A. Energy of moving water on a beach (Schiffman, 1965).



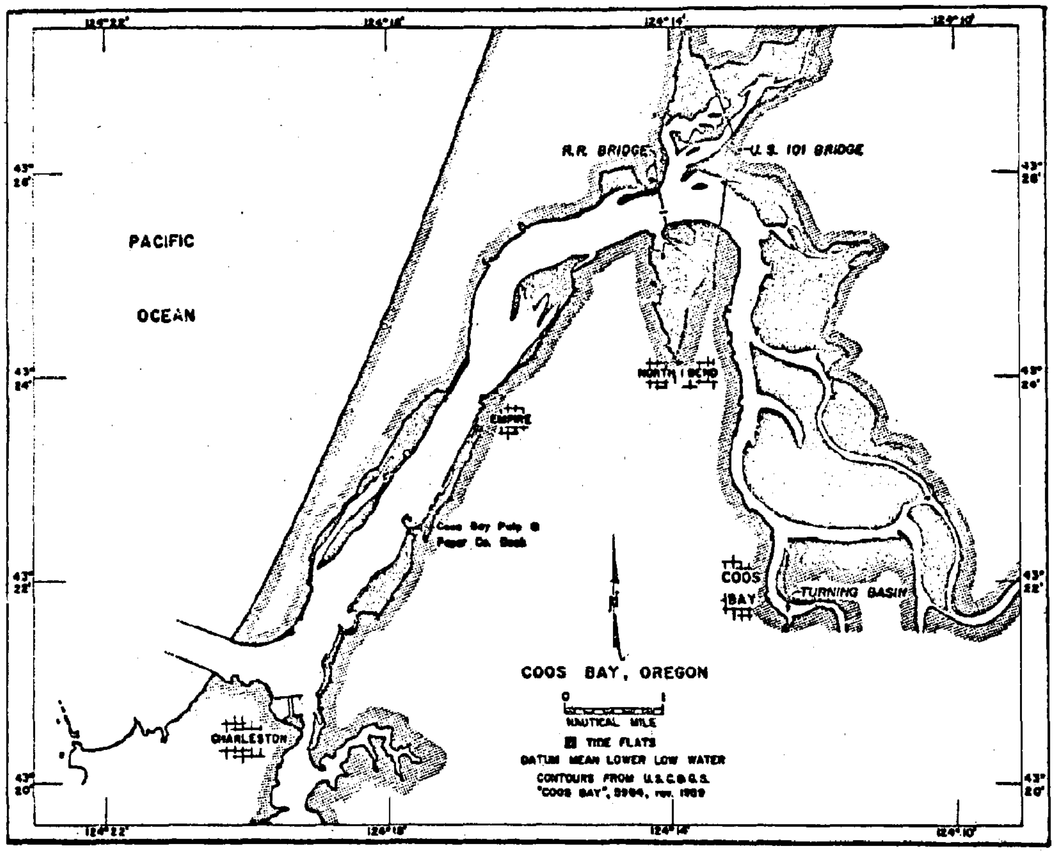
Relationship of the average density of individuals of *Mercenaria mercenaria*, the bottom type, and the current in Chincoteague Bay, Maryland. (After H. W. Wells, 1957.)

Fig. 6B. Action of current energy in control of sediment size and clam growth (Ager, 1963).


COASTAL ENERGY LEVELS
High
Moderate
Low
Moderate
High
Low
Low
Moderate
Low
High
Moderate
High

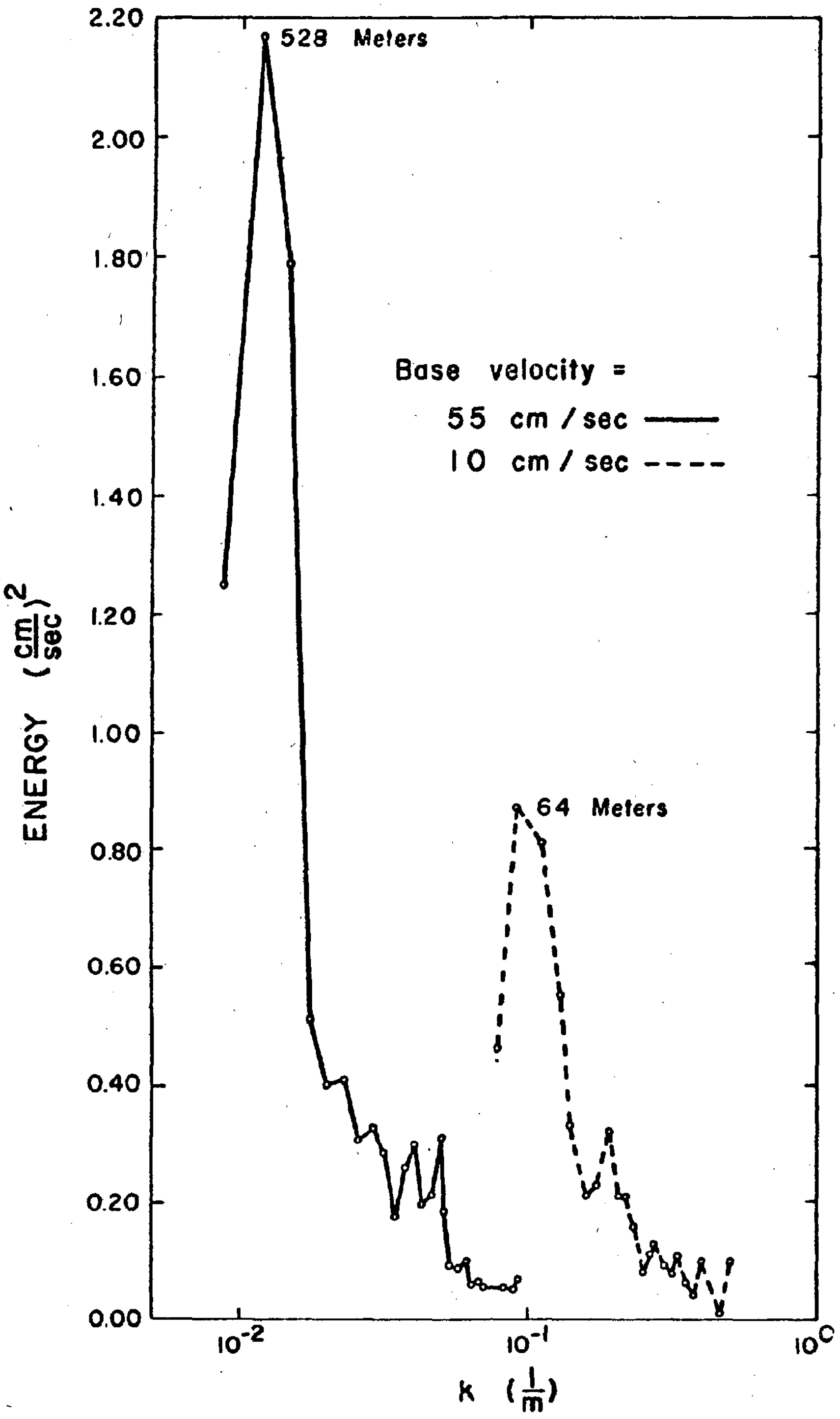
—Coastal energy levels of the U. S. South Atlantic and Gulf of Mexico (Tanner, 1960).

Fig. 6C. Classification of coastlines according to wave-current energies (Linton,1968).


124°22'
124°18'
124°14'
124°10'
43° 26'
43° 24'
43° 22'
43° 20'
PACIFIC
OCEAN
R.R. BRIDGE
U.S. 101 BRIDGE
NORTH BEND
EMPIRE
Coos Bay Pulp & Paper Co. Dock
COOS BAY
TURNING BASIN
CHARLESTON
COOS BAY, OREGON
0
1
NAUTICAL MILE
TIDE FLATS
DATUM MEAN LOWER LOW WATER
CONTOURS FROM U.S.C.&G.S.
"COOS BAY", 5984, rev. 1959

Map of Coos Bay showing location and extent of tide flats.

Fig. 6D. Oregon estuary in which tidal energy measurement was made (Blanton, 1964).



Energy spectra for high and low tidal velocities at the U.S. 101 bridge.

Fig. 6E. The distribution of energy according to size of eddy in Coos Bay, Oregon at two stages of the tide, data used in computing energy dissipation from the tide (Blanton, 1964).

ecosystems. For example, two estuaries with the same salinity and mixing pattern are entirely different ecologically if the nutrition of the river contribution is different or the seasonal timing of temperature is different. The salinity classification does not include enough factors for general estuarine classification.

The use of differences between freshwater heads and tidal heads to get exchange coefficients is a means of using potential energy for estuarine classification (Urban and Masch 1966). Although this is only one type of energy influencing estuarine systems, it has been useful for engineering design and hydrographic modeling. Blanton (1964) measured the energy dissipation from the tide in an Oregon estuary (Coos Bay) (Fig. 6D, 6E).

Another kind of classification is based on man's interaction with the estuary as part of the land system rather than on properties of the estuarine system alone. A practice of classifying estuaries as A, B, C, D, etc. according to quality of use was developed by governmental agencies to regulate the permissiveness regarding waste disposal. This pattern has been extended from streams into estuaries in many states. Often this usage classification has been made for shores without regard to the unit of recirculating water where such a classification might have some workability. Often the typing refers to safety for shellfishing in the presence of sanitary wastes containing fecal bacteria. Sanitary classifications probably provide some idea of the degree of outside nutrient fertilization. Use classifications are of little value for the management of marine systems for optimum benefits of a harmonious coupling of Man and nature. The resource and use must make sense together.

Where man's destructive use of the estuary becomes dominant, as with low quality classification (D) where harbors have received multiple wastes of many industries in high concentration, the typing may well characterize a new "stinko" estuarine type. In general, however, the classification makes no distinctions between kinds of ecological systems, and thus provides no guide to the kinds of resource use possible. Our knowledge of estuaries should allow us to do much better and provide a sounder ecological basis for estuarine management.

All of these previous efforts at classification suffer from the same difficulty of including only part of the predominant phenomena and factors involved. Elsewhere in affairs of science and man, complexity of different processes have been amenable to unified consideration by the use of the concepts of energy flow. Energy is a great common denominator measuring processes of all kinds. Thus we attempt next to combine the roots of the historical contributions to classification through a general energy classification.

THEORETICAL BASIS FOR AN ENERGY CLASSIFICATION

The classification by energy allows such different features of systems as light, tide, pollution, fertilization, harvests and thermal degradation to be considered under one common denominator, that of potential energy flow. Different types of systems result when the energy flows are different in character, and the organisms that control the systems show these differences in their adaptations and diversities. Our classification is given in Table 1. Consider some theoretical aspects of the system.

Table 1: A classification of coastal ecological systems and subsystems according to characteristic energy sources.

Category	Name of type	Characteristic energy source or stress
A. Naturally stressed systems of wide latitudinal range		High Stress Energies
	A-1. Rocky sea fronts and intertidal rocks	breaking waves
	A-2. High energy beaches	breaking waves
	A-3. High velocity surfaces	strong tidal currents
	A-4. Oscillating temperature channels	shocks of extreme temperature range
	A-5. Sedimentary deltas	High rate of sedimentation
	A-6. Hypersaline lagoons	briny salinities
	A-7. Blue-green algal mats	temperature variation and low nighttime oxygen
B. Natural tropical ecosystems of high diversity		Light and Little Stress
	B-1. Mangroves	light and tide
	B-2. Coral Reefs	light and current
	B-3. Tropical Meadows	light and current
	B-4. Tropical inshore plankton	organic supplements
	B-5. Blue water coasts	light and low nutrient

Table 1 (cont'd.)

Category	Name of type	Characteristic energy source or stress
C. Natural temperate ecosystems with seasonal programming		Sharp seasonal programming and migrant stocks
	C-1. Tidepools	spray in rocks, winter cold
	C-2. Bird and Mammal Islands	bird and mammal colonies
	C-3. Landlocked sea waters	little tide, migrations
	C-4. Marshes	lightly tidal regimes and winter cold
	C-5. Oyster reefs	current and tide
	C-6. Worm and clam flats	waves and current, intermittent flow
	C-7A. Temperate grass flats	light and current
	C-7B. Shallow Salt Ponds	small waves; light energy concentrated in shallow zone
	C-8. **Oligohaline systems**	saltwater shock zone, winter cold
	C-9. Medium salinity plankton estuary	mixing intermediate salinities with some stratification
	C-10. Sheltered and stratified estuary	geomorphological isolation by sill
	C-11. Kelp beds	swells, light and high salinity
	C-12A. Neutral embayments	shelfwaters at the shore
	C-12B. Coastal Plankton	eddies of larger oceanic systems
D. Natural Arctic **Eco**systems with ice stress		Winter ice, sharp migrations and seasonal programming
	D-1. Glacial fiords	icebergs
	D-2. Turbid outwash fiords	outflow of turbid icewater lens

Table 1 (cont'd.)

Category	Name of type	Characteristic energy source or stress
	D-3A. Ice stressed coasts	winter exposure to freezing
	D-3B. Inshore Arctic ecosystems with ice stress	ice, low light
	D-4. Sea ice and under-ice plankton	low light
E. Emerging new systems associated with man		New but characteristic man-made energy sources and/or stresses
	E-1. Sewage waste	organic and inorganic enrichment
	E-2. Seafood wastes	organic and inorganic enrichment
	E-3. Pesticides	an organic poison
	E-4. Dredging spoil	heavy sedimentation by man
	E-5. Impoundment	blocking of current
	E-6. Thermal pollution	high and variable temperature discharges
	E-7. Pulp mill waste	wastes of wood processing
	E-8. Sugar cane waste	organics, fibers, soils of sugar industry wastes
	E-9. Phosphate wastes	wastes of phosphate mining
	E-10. Acid waters	release or generation of low pH
	E-11. Oil shores	petroleum spills
	E-12. Piling	treated wood substrates
	E-13. Salina	brine complex of salt manufacture
	E-14. Brine pollution	stress of high salt wastes and odd element ratios

Table 1 (cont'd.)

Category	Name of type	Characteristic energy source or stress
	E-15. Petrochemicals	refinery and petrochemical manufacturing wastes
	E-16. Radioactive stress	radioactivity
	E-17. Multiple stress	alternating stress of many kinds of wastes in drifting patches
	E-18. Artificial reef	strong currents
F. Migrating subsystems that organize areas		Some energies taxed from each system

In the presentations that follow, a principle of classification is used which gives recognition to whatever influence is most prominent whether it be physical, biological, geological or derived from the actions of man. The common denominator for measuring the amount of influence is energy. All processes by man or by nature are measurable by the amounts of potential energy in Calories which have been passed through the system doing work. The kinds of energy that usually dominate the coastal systems are of three main types (Fig. 8A).

1. Light energy drives photosynthesis of the plants and supports the food chains that support biological populations. Where other energy sources are relatively minor, the light energy acting through plants so characterizes the system that it is appropriate to recognize the productive plant in the classification. Thus we have Eelgrass systems, Phytoplankton systems, Turtlegrass systems, Kelp beds, etc.

2. Organic fuels constitute a second regular energy source to the coastal ecosystems. Many rivers, for example, carry loads of organic matter from the fields and forests which serves as the food for bacteria and higher animals. Some of these fuels are wastes from man's emerging system. Others are entirely natural such as the organic matter from swamps or mangrove coasts.

3. Mechanical energy is the absorption of fluid momentum of the winds, waves and tides and is another environmental source of energy, which is responsible for many of the phenomena of the system. A beach, for example, receives the pounding of incoming waves that so predominate the system that the sedimentation, the organismal adaptations and chemical phenomena are determined and coupled.

Often, when other energy flows are dominant such as light-driven photosynthesis, the physical energy augments particular processes as an auxiliary source. Thus the turbulence of physical stirring serves to augment nutrient circulation, making special pumping mechanisms by organisms unnecessary, and allowing other properties to be developed instead. Such differences are implemented by substitution of species.

The flows of energy are channeled according to the biological, chemical and geological structures of the system that are in turn maintained by the system or introduced from the outside (and thus are energy sources). The sedimentary structure of a beach is maintained by the properties of breaking waves. The patterns of plankton are maintained by circulation of waters and the behavioral responses of the animals.

Energy Flow Diagrams

The representation of energy flows may be done with energy flow diagrams (Fig. 8A, B) using the symbols in Fig. 7. Energy flows from potential energy storages (Circles) or from external energy sources. All potential energy which does work must divert some of its flow into dispersed heat as shown by the arrow-ground symbol, which diagrams the second energy principle. External energy sources provide energy in programs that are characteristic of the situation. The energy budgets of most estuarine systems are sketchily known so that quantitative values are available in only a few cases. Certainly completion of the main features of the energy diagrams with quantitative data on flows and programs of input are developing understanding and among the first needs in management.

Where a flow requires a second flow as in a chemical reaction, in a process incorporating essential parts, in a process requiring work from a second source, etc., the second flow of energy passes into heat while making possible potential energy flow from the first source. This is indicated by the work gate symbol (pointed block). Such a symbol represents multiplication of two flows and the process of varying the force of one while holding the second constant provides a hyperbolic output response of the interaction. The quantitative aspects of energy diagramming and other systems languages are not treated here except to show the relative dominance of particular flows that dominate the principle classes of coastal systems. These diagrams may help to clarify verbal statements. A system is an organization of component participating parts and flows, and the diagrams help to clarify the organization of these parts.

Names

Although dominant energy inflow should determine the classification assigned to a system, naming of systems needs to be familiar, readily attached to our experiences and easily remembered. Names, therefore, are common English words which describe or are associated with the dominant energy influences. The quantitative accounting of the proportion of total phenomena including physical, chemical, biological, geological and man-made processes is energetic and may be diagrammed similarly. The flow of energy from potential energy into useful work is the great common denominator.

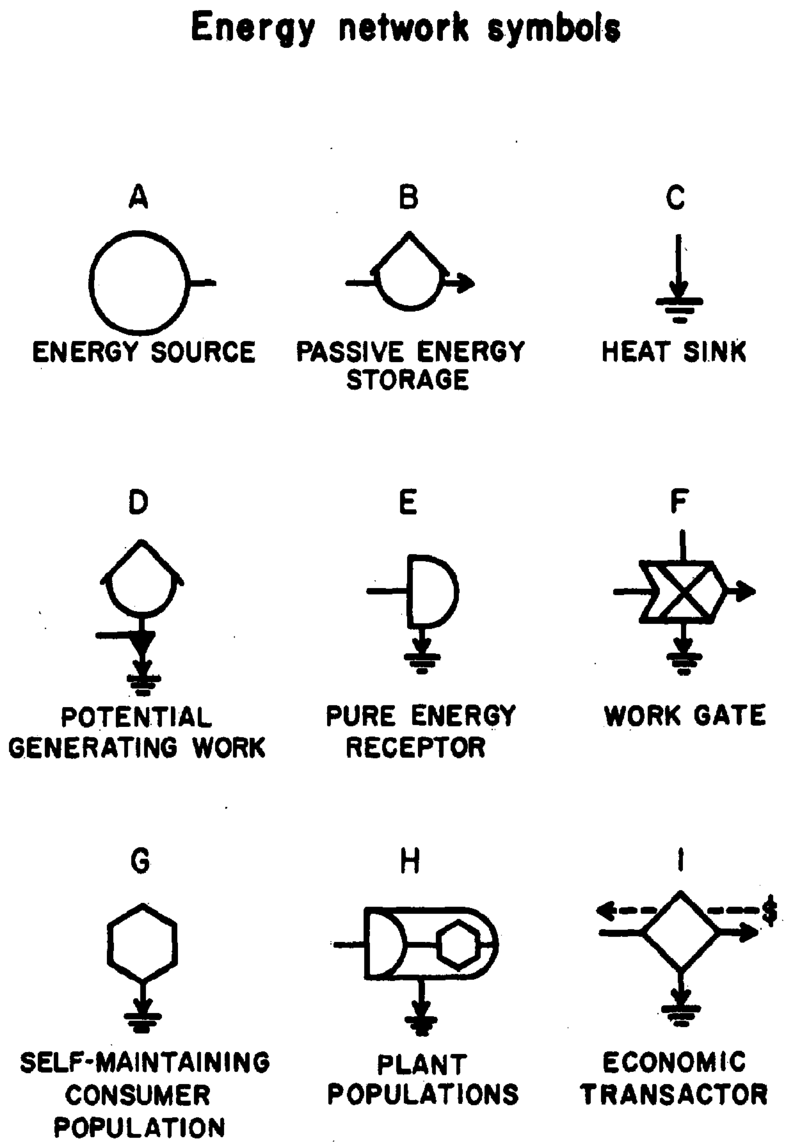

Energy network symbols
A
ENERGY SOURCE
B
PASSIVE ENERGY STORAGE
C
HEAT SINK
D
POTENTIAL GENERATING WORK
E
PURE ENERGY RECEPTOR
F
WORK GATE
G
SELF-MAINTAINING CONSUMER POPULATION
H
PLANT POPULATIONS
I
$
ECONOMIC TRANSACTOR

Fig. 7. Symbols of energy flow diagrams(Odum, 1967c).

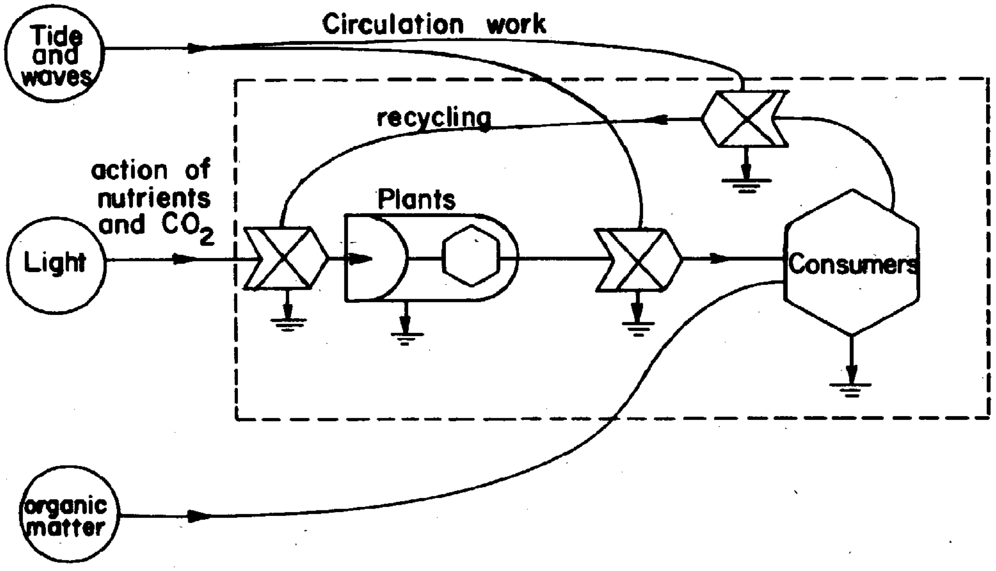

Tide and waves
Circulation work
recycling
action of nutrients and CO_2
Light
Plants
Consumers
organic matter

Fig. 8A. Three main sources of potential energy for estuarine ecosystems. Symbols are given in Fig. 7.

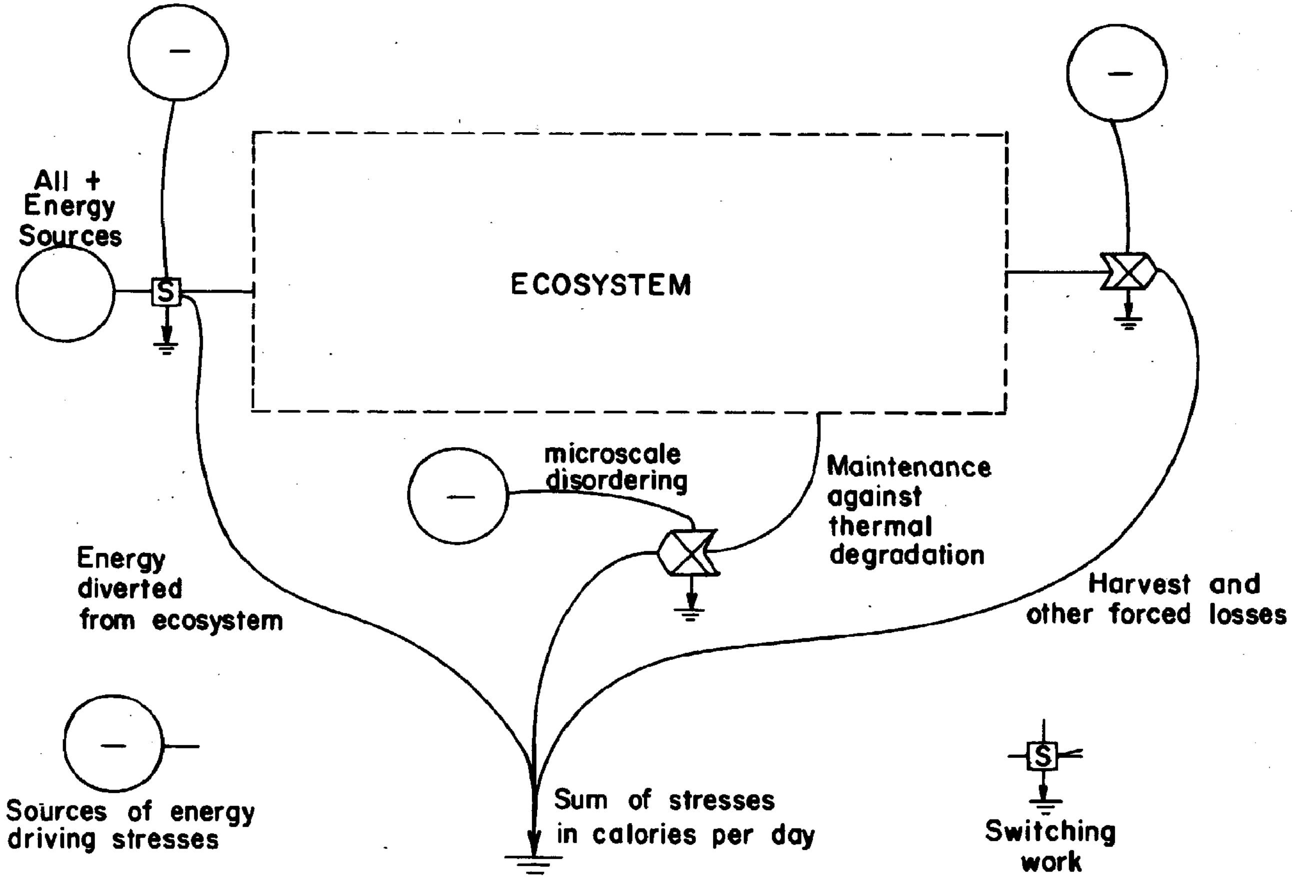

All +
Energy
Sources
S
ECOSYSTEM
microscale
disordering
Maintenance
against
thermal
degradation
Energy
diverted
from ecosystem
Harvest and
other forced losses
Sources of energy
driving stresses
Sum of stresses
in calories per day
S
Switching
work

Fig. 8B. Main sources of stress in estuarine ecosystems. Stress is defined as potential energy diversion or drain.

Boundaries

The boundaries of an estuarine system may be the natural boundaries of a shore line if that shore encloses a system of components. Usually, however, one system connects with another so that boundaries are not sharp. There are usually flows from one system to another but it may be convenient to draw a boundary when the cycling and organizational processes within the system are of greater magnitude than the input and output flows.

Systems and Sub-Systems

All systems are made up of sub-systems, lesser but recognizable units with their own characteristic flows and structures. A residential district is a subsystem of a city. A mud flat or a submerged grass bed are examples of subsystems of an estuary. Sometimes the type of system in one area is a major system but becomes a minor subsystem in some other area. Most partially-enclosed basins on the coasts are not single systems for our purposes, but include recognizable sub-systems which require separate treatment for understanding and management. The coast lines of the United States have strings of systems and sub-systems alternating according to the external energy flows available at different locations.

Stress as Energy Drain

When an energy flow drains structure and energy away from another flow it contributes to the character of that system, although it may be detrimental in the sense of eliminating structures and patterns that would have developed due to some other energy flow. For those conscious of biological properties, growths and populations, there are many energy flows of great severity that drain energies away from biological productions either by destruction or by requiring defensive adaptive work by animals. Low diversities of organisms accompany the development of special adaptations of the organisms that do maintain a system. Whether positive or negative, energy flows are characterizing the system. Pollutional actions are one of the many kinds of energy flows that may modify a system's structure and processing in special ways (Fig. 8B).

Emergent New Systems Coupled to Man's Influence

Emerging in response to dominant special new energy flows from man's civilization are characteristic complexes of organisms, chemical properties and geological parameters that constitute new estuarine systems. The characteristic patterns found when sewage is running into sea water or the complex near pulp mill outfalls are examples of new systems that may be expected to reoccur whenever an estuary is dominated by one of these special inputs due to man. These new systems have had little time to develop special organisms by evolution although the micro-organisms are capable of rapid mutation and selection. Through preadaptation, organisms may exist on earth in fresh or salt water which will find conditions of the new flow adequate and growth-promoting. The testing of the suitability of organisms to these new conditions is going on continuously by the trial and error of animal migrations without any aids from man. There is some reason to hope that one of our new pollution systems which has inadequate processing, cycling and order now may in time become a better self-controlled pattern as more organisms evolve or emigrate to develop the variety and specialists of the system. In Table 1 are recognized in the classification some of the emergent new systems where examples exist that provide evidence of special character. In defining the emergent new systems associated with new inflows from man, we do not necessarily indicate whether the new system is good or bad, such judgement being related to considerations such as the type of system displaced, the system of man and nature desired at that point and the meaning of the change for the survival of man.

New disturbed systems which may seem harmful by displacing valuable natural systems, if knowledge develops, may be managed with additional controls towards some useful and beneficial purposes. In this report we seek only to recognize the controlling energy flows, base our classification on this natural basis and organize our knowledge therewith.

NET SOURCE-STRESS ENERGIES AS A SCALE FOR ESTUARINE CLASSIFICATION

In considering latitudinal and emerging ecosystem types, the presence of characteristic types is apparently related to the energy available for supporting special systems. Consider the following theoretical reasoning which underlies the classification of American estuaries. The following summarizes current ecological theory.

Relation of Energy to Specialization and Diversity

It is a well established principle in ecology that among populations of organisms of different species capable of exponential Malthusian growth, if not organized in some way to prevent competition, one species will exclude the other. This is so because the one with an edge in reproductive rates will, under the conditions, feed back its resources into more individuals, gaining an ever widening supremacy in numbers and ability to use the resources in comparison to its competitor. Thus in various kinds of simple situations in laboratory or in disturbed situations in nature, competitive exclusion is the result.

If, however, there are additional species that serve to regulate and control, if there are programs of behavior built into the species involved, or if other means such as specialization prevent competitive exclusions, then the pattern of many species is possible. There is diversification and specialization, and the system as a whole may have higher efficiencies in its total effect although energies are spent in the controlling and organizational process. Organization is thus measured in the control preventing competitive exclusion and permitting specialization. The amount of specialization and organization possible depends on the energies available after stress and basic maintenance of a system is covered.

Thus any disturbances and stresses introduced by climate, fluctuation in external condition or actions of man serve to detract energies from that capable of developing organization and diversity. Competitive exclusion increases and species diversity must decline. Diversity is thus useful as an index of the amount of stress whether natural, induced by pollution, or other influence. In one stress location a particular species may prevail and a different one in another location, but both are possible only when there is less energy drain and enough remaining for organization to support both.

The opportunity for a species, in ecological jargon, is called the niche, a term that refers to the input and output connections provided by the system and to the role of the species which adapts to these inputs and outputs. More niches are possible with more energy beyond stress costs because more complex networks can be organized by energies spent on control mechanisms.

In general, availability of energy for organization and diversity divides the flows of energy among many kinds of species so that there is little for any one. Thus, potentials for food harvest for man are not increased even though the total productivity of all the species tends to be large. Stresses often channel energies into high yields of a few products which are succeeding in competitive exclusion. Where stress is high and diversity is small, the estuarine system tends to have a few dominants, to support large fisheries based on one or two species. Because the system is not finely tuned in adaptation, it tends to cover wide ranges in latitude. These systems tend to take human disturbance readily because of their specialization for change, rapid replacement and programming for severity.

The complex systems have great diversity of specialists for mineralizing various organic chemical substances of the ecosystem and from man's waste. A property of the diverse system is effective mineralization and water cleaning processing. Stresses that tend to reduce the diversity eliminate much of this ability for diverse microbial and chemical processing by the organisms. Thus there is an inverse relationship of mineralization and food yield tendencies of ecosystems.

Size, time and location of systems are also involved. If there is an isolated small estuarine system, it may not have had the size and time to evolve independently as many kinds of species as it might support under the conditions of energy source and stress. If, however, species which have developed the same kinds of adaptation elsewhere can be moved in, there may be an increase in the diversity and organization possible. Particularly in isolated situations like Hawaii, there may be more simplicity than energies are capable of supporting. When systems are very small the probability of re-establishment is smaller relative to probabilities of extinction due to normal fluctuations of small simple systems. The theory that the balance of energy of source minus stress controls diversity suggests a pattern of different estuarine types represented in Fig. 9. On the horizontal axis is represented energy source and on the vertical axis energy stress (drains). Diversity and organization is highest where energy sources are high and stresses low as in many tropical situations or in many situations in oceanic temperate locations and least in arctic situations, in areas of great salinity shifts, or in areas of large disturbance by man.

Diagram of Latitude and Salinity Stress

In estuaries, the stress of the fluctuating salinity and latitudinal temperature shifts are main influences that operate to control diversities and the variety of ecosystem types. In Fig. 10 the amount of salinity fluctuation is indicated on the horizontal axis and latitude is indicated on the vertical axis. High latitude has severe seasonal temperature changes for which surviving programs are necessarily adapted. In general the higher latitudes have about half as much light energy per year to use towards maintaining structure as compared with the tropics so that the combination of less energy and more temperature stress allows less energy for specialization and organization.

The section in the lower left with low stress from temperature and salinity has high diversities in each system and a high diversity of possible systems adapting each one in a finely tuned manner to local circumstances so that there are many more kinds of sub-types. The upper right section of the diagram with high salinity variation is very low in species and tends

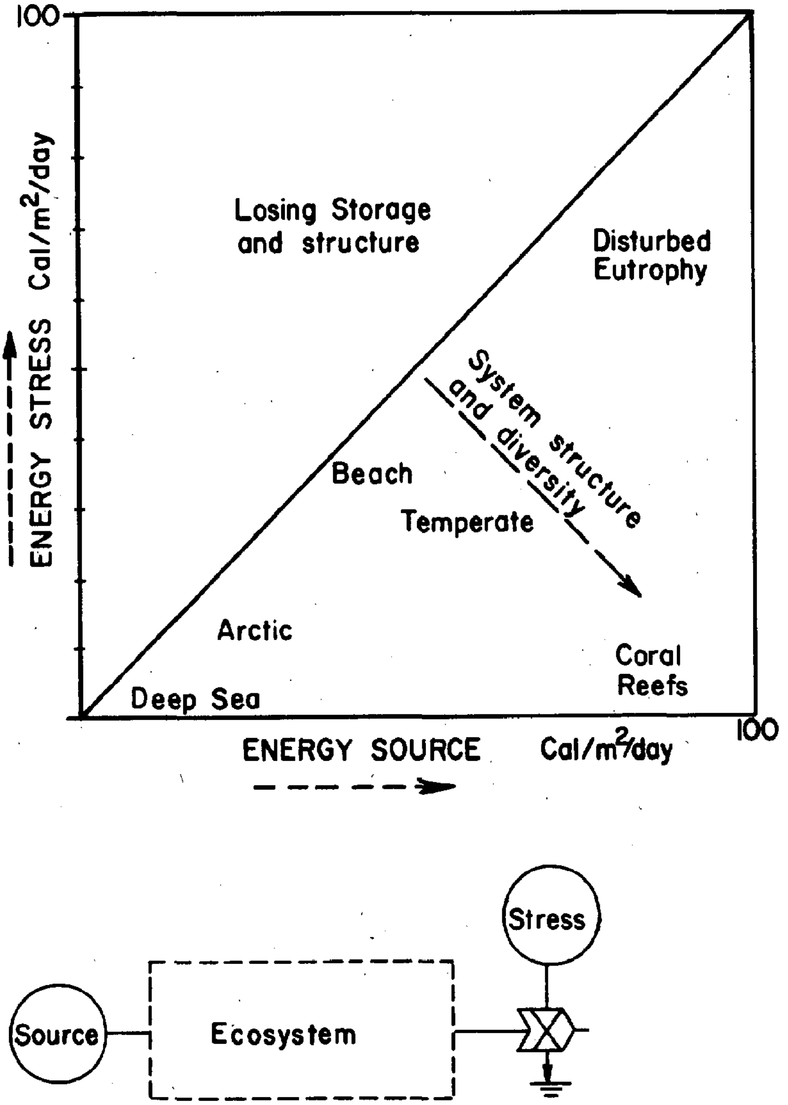

100
ENERGY STRESS Cal/m²/day
Losing Storage and structure
Disturbed Eutrophy
System structure and diversity
Beach
Temperate
Arctic
Coral Reefs
Deep Sea
ENERGY SOURCE Cal/m²/day
100
Stress
Source
Ecosystem

Fig. 9. Diagram for showing ecosystems as a function of their useful energy sources and detrimental stress. The space between the plotted point and the diagonal line is a measure of the energy for structure and diversity.

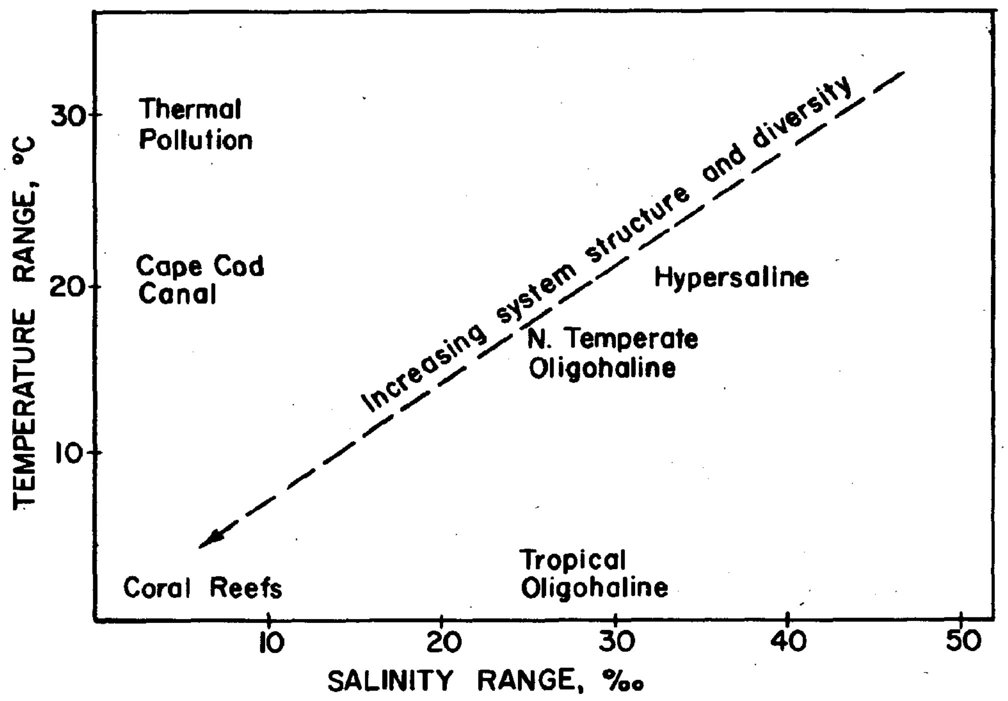


Fig. 10. Graph of temperature and salinity ranges for diagramming stress and diversity of ecosystems.

to have only a few types. Typing is not only simpler, but management planning may be more readily studied.

Latitudinal Differentiation

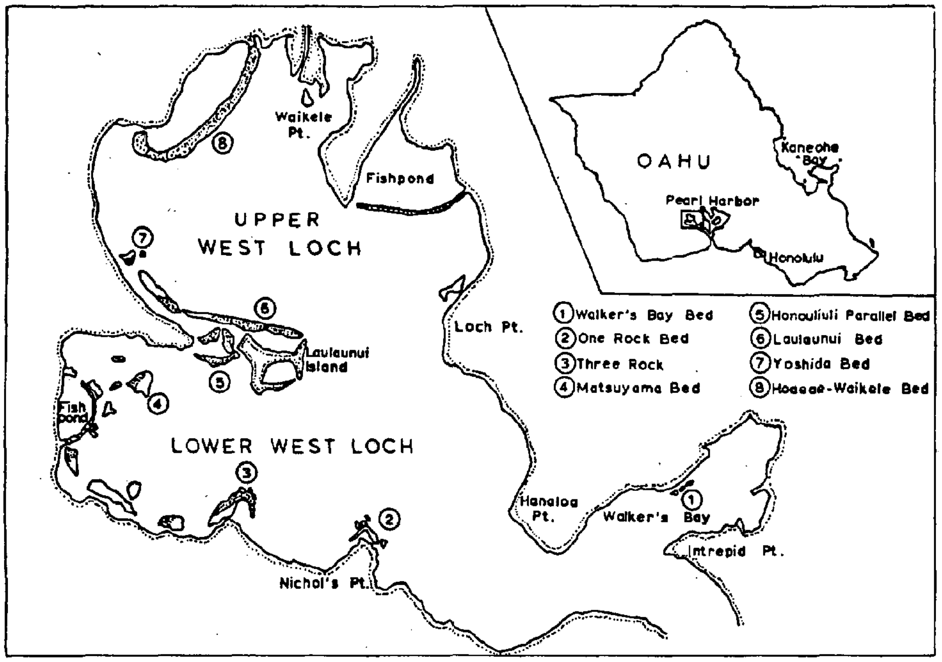
In systems in which stress is large, the energies for finely tuned diversity, specialization and organization do not exist and specialization of faunas with latitude do not develop. Thus in natural areas which have high wave energies like beaches, in sharply fluctuating salinity situations, or in situations of extreme pollution, latitudinal differences disappear as the adapted differentiated systems are displaced. Highly stressed systems can therefore be classed according to the stresses to which their components must adapt, but not according to latitude. One of the most striking examples is the prevalence of Crassotrea virginica (the eastern oyster) reef system in Pearl Harbor, Hawaii where sharp stresses from salinity fluctuation and from pollution bring in the general stressed pattern system of the east coast of the United States (Figs 11-13).

Another is the severe fluctuation of temperature in the Cape Cod Canal which simplifies attached communities, producing the ubiquitous green algal associations that one finds also in polluted harbors at San Juan, Puerto Rico, or the naturally stressed intertidal zones of Venezuela (See Chapter A-1) or Alaska (Hubbard, 1968).

Thus the first main division of our classification consists of natural systems of wide latitudinal distribution associated with high stress energies of natural origin. For similar reasons we group most of the emerging new systems associated with new kinds of stress from man also without much latitudinal variation. In the man-stressed systems, there is an additional factor of inadequate time for evolution of adapted specialists.

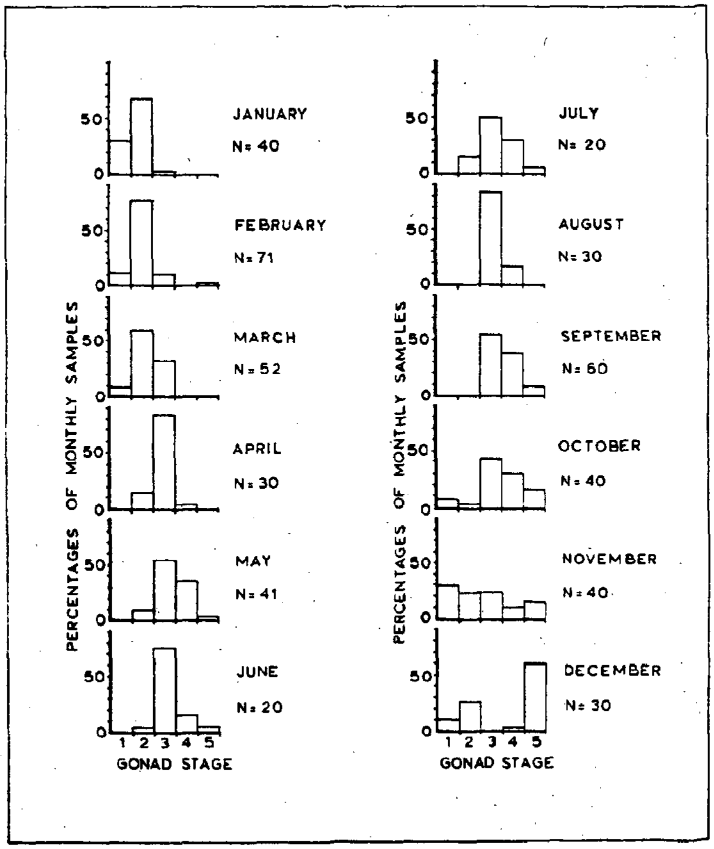
As one moves away from the high energy beaches and salinity-shocked river mouths, the stress diminishes and the differentiation is with latitude and temperature programming. The eastern United States in general has severe fluctuations of salinity and temperature in its inner estuaries and has very little zonation from Maine to southern Texas. In outside sea waters, however, temperatures and salinities are far more constant and there are characteristic biogeographical zones. Around each cape there are species substitutions as at Cape Cod, Cape Hatteras, Cape Canaveral, etc., whereas in the inner estuaries the substitutions are fewer. As one moves south on the east coast, temperature and tidal stresses do decrease although salinity variations often increase in the subtropics because of erratic rainfall. The interplay of the fluctuation type of energy stress seems to predict whether generalized stress systems prevail or whether characteristic latitudinal types result.

The flows of estuarine energy on earth may be considered conveniently in three latitudinal groupings, tropical, temperate and arctic. Tropical systems have higher drains of thermal dissociation requiring more respiratory work maintenance, but programs of temperature change are often less variable. Light energy is greater on the yearly average and more regular. Tidal and wave energies are usually less, although exceptional energies develop in infrequent hurricanes. Arctic systems have extreme shifts in light and dark programs of solar insolation, variable temperature and the


Waikele Pt.
⑧
Fishpond
UPPER WEST LOCH
⑦
⑥
Laulaunui Island
⑤
④
Fish pond
LOWER WEST LOCH
③
②
Nichol's Pt.
Loch Pt.
Hanaloa Pt.
Walker's Bay
①
Intrepid Pt.
OAHU
Kaneohe Bay
Pearl Harbor
Honolulu
①Walker's Bay Bed
②One Rock Bed
③Three Rock
④Matsuyama Bed
⑤Honouliuli Parallel Bed
⑥Laulaunui Bed
⑦Yoshida Bed
⑧Hoaeae-Waikele Bed

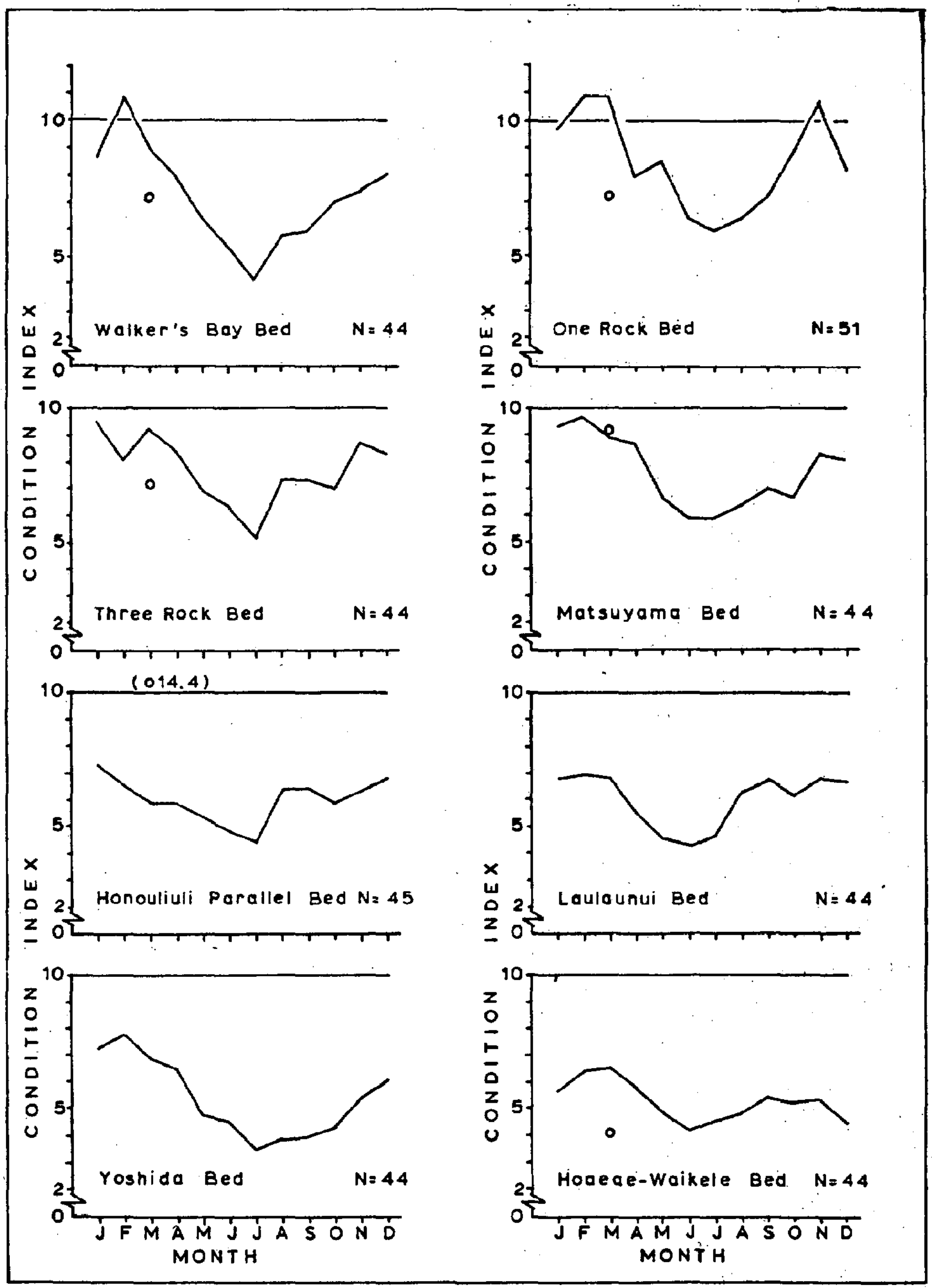
Location of eight oyster beds sampled for condition in West Loch, Pearl Harbor, Oahu, Hawaii. Names of oyster beds after Sparks, 1963.

Fig. 11. Oyster reefs (*Crassostrea virginica*) in a disturbed tropical environment (Sakuda, 1966b).



-Monthly gonad stages of oyster (*C. virginica*) in West Loch, Pearl Harbor, Hawaii.

Fig. 12. Storage pattern in a tropical regime.



Average monthly condition indexes of American oysters from eight beds in West Loch, Pearl Harbor, Hawaii. Circles represent C. I. values presented by Sparks (1963) for samples from the same beds (North Gate Bed of Sparks compared to Matsuyama Bed from this study).

Fig. 13. Oyster characteristics in a tropical regime (*Crassostrea virginica*) (Sakuda, 1966b).

action of ice. The temperate systems are characterized by moderate light pulse with season, moderate temperature ranges, moderate temperature, large tides and large waves.

Power and Communication Connectives

It is a property of most estuarine systems that they are coupled to other nearby systems of freshwater or open sea by means of flows from one to the other which have controlling effects. Examples are the migration of populations of fishes with reproduction one place, nursery growth in a second place and, sometimes, further action as adults in yet another place. These populations are participating as components in more than one system andby the timing of their participation they serve to even out energy loads or place controlling energy drains which accentuate fluctuations. If by such timing of their life cycles these populations arrange for special inputs to their own processes, they are assured a continuing role. Insuring continued support from the system, the migrant provides some control service in exchange for its effect of feeding. The migrations of salmon, shrimp and other organisms are examples of inter-power system connectives, in the same sense that telephone and power lines connect cities. The roles of these flows in one system are that of an outside energy flow, although sensible management requires that consideration of the connective as a whole mechanism be also considered.

Power transmission systems are a property of systems with regular programs of production and stress. They permit more diversity and efficiency in a locality than could be supported through seasons of the year of minimum energy and maximum stress. The phenomenon of migrating major pulses increases generally with latitude associated with light and temperature cycles although there are major pulses in tropical zones wherever such patterns as monsoons and shifting doldrum belts change rainfall and salinity regimes.

Much emphasis has been placed in a century of work on fishes like salmon,that reproduce in freshwaters and move into the sea during their weight gains, and components like the Anguilla eels or Penaeid shrimp that reproduce at sea and move landward during weight gain. An examination of all these moving populations suggests that the critical aspect of survival is synchronizing the populations' main energy need in phase with a strong pulse of energy availability. Whether it is king crab in Cook Inlet, Alaska (Bright, Durban, Knudsen, 1960), shrimp of the bays of Texas (Odum, 1967b), or salmon passing through lakes and estuaries during their period of most rapid weight gain (see Chapter F), the patterns seem similar.

In earlier studies security of the reproduction process has been emphasized. In the last century, marine fish hatcheries were developed. They failed because no one had any idea of the numbers involved in these processes and drop-in-the-bucket levels were involved in the hatcheries. The public still retains this kind of view. Predictions of salmon and many other stocks are still being developed on the assumption that the limiting factor in stocks is the number of young launched. Where a river is blocked to salmon or a bay blocked to shrimp, reproduction does limit, but what about the usual pattern? For salmon, and many other heavily studied species data do not exist fully to prove the theory of population as the limit at maximum energy demand stage (per population). Theories in vogue in management agencies permitted management of species to be done independently of management of the whole system.

Not only are there migrations from the sharply pulsing estuary to the lesser pulsing open sea systems, but there is a general latitudinal migration of large oceanic and coastal fishes north during the productive season and back south during the low productive season, thus helping to spread the seasonal energy pulse more evenly over the oceans and coasts.

The five main divisions of our classification are given in Fig. 14. Latitudinal differences exist in the highly stressed systems of natural and man-disturbed types, but these are considered as variants rather than as entirely different systems. Where salinity, pollution, and wave stresses are not great, latitudinal differentiation occurs with quite distinctively different systems recognizable with latitude related to temperature levels, to seasonal programming, and to migrating populations.

Plankton and Bottom Differentiation

Even in the freshwaters, one readily classifies systems according to the role of the bottom subsystems. For example, many recipes for fish pond management concern the competition between plankton systems and benthic plant dominated systems, the one shading out the other or taking away nutrients because of its ability to hold a motion relative to the moving water.

In the coastal systems we may distinguish four main classes of systems related to depth and the role of the bottom. Seaward of the coastal systems if one is at the continental slope the bottom of the seas may drop sharply away so that the surface ecological system has no bottom. The phenomenon of the deep scattering layer develops and one has the surface system coupled to a complex migration of shrimps and other animals moving up and down each day and night. In general any system with a deep scattering layer subsystem under it is outside of the scope of our effort to classify the coastal systems except where it is continually washing up on shore (Chapters B-5, C-12).

For purposes of classification we separate those systems with sufficient clarity and shallow water so that the bottom attached plants have 50% or more of the plant photosynthesis. Many of the salt ponds of New England have important bottom communities as do the bays of Texas. Shallow productive systems bathed with tidal waters and little salinity fluctuation have high productivities and moderately high diversities. Among these systems and subsystems are the eelgrass beds of the temperate latitudes and the turtle grass meadows of the tropics.

When the bottom is too shaded for major plant production the photosynthesis is by the phytoplankton and the food chains are based on zooplankton and zooplankton-feeding fishes as well as on benthic filter feeders, the clams, mussels and oyster reef subsystems. When the water is so deep that the bottom becomes unimportant, the main consumer system is that of the plankton food chains as through herring-like fishes. Most estuaries have fairly equal roles of benthic and swimming consumer components because of

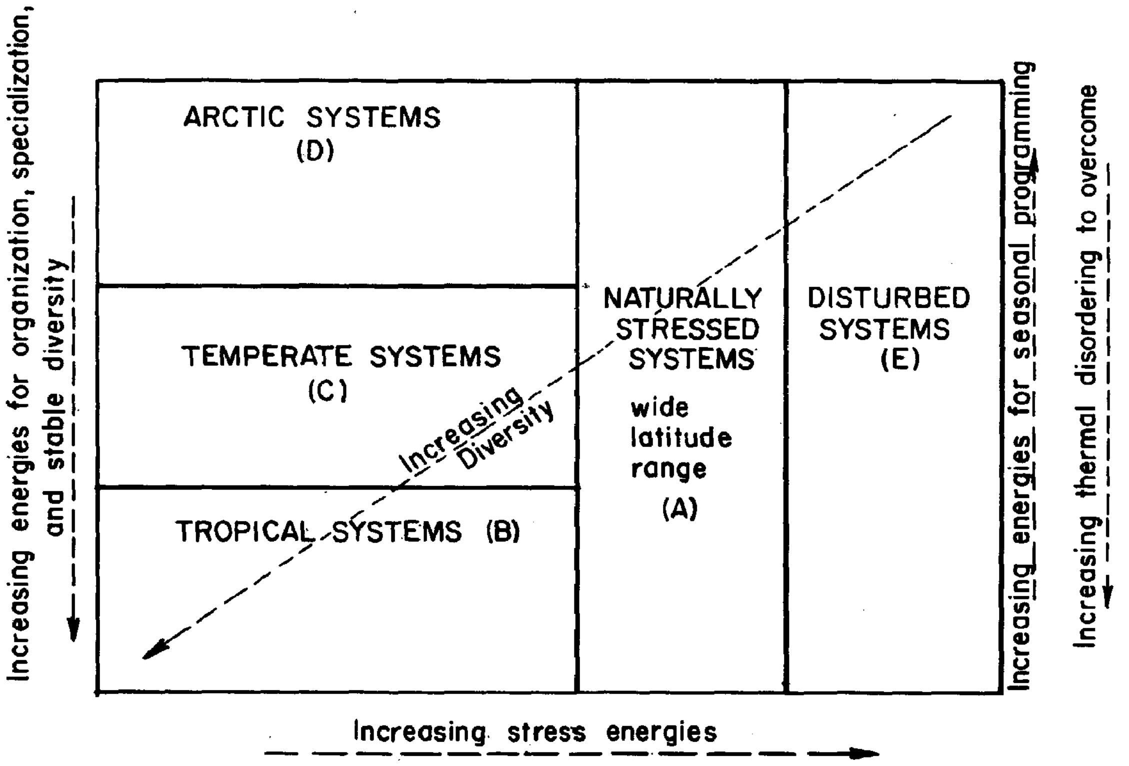

ARCTIC SYSTEMS (D)
TEMPERATE SYSTEMS (C)
TROPICAL SYSTEMS (B)
NATURALLY STRESSED SYSTEMS
wide latitude range
(A)
DISTURBED SYSTEMS (E)
Increasing Diversity
Increasing energies for organization, specialization, and stable diversity
Increasing stress energies
Increasing energies for seasonal programming
Increasing thermal disordering to overcome

Fig. 14. Relationship of the main categories of ecosystem classification to latitudinal factors and other stress.

the intermediate depth of the bottom. The benthic consumers are a subsystem that varies in its importance, being a minor component in deep estuaries and a major system of energy processing on clam flats.

West Coast and East Coast Comparisons

It became apparent soon after the state surveys were begun that the systems of the east and west coast could be placed under the same categories even though there were different names of species dominating in many instances. We confirm, therefore, the "parellelism"' generalizations of Thorsen (1957, 1958).

On both coasts salinity changes are a main stress. Temperature fluctuation on the east coast is due to sharp shifts in strongly flowing air masses, whereas on the west coast the stress comes from upwelling and injections of cold water from the sea. In general the stress severity of the east coast was greater so that west coast estuaries often had several species occupying the role of a single species on the east coast. In Table 2 are some equivalents suggested among dominant and commercially important species of fish and crustacea from the east and west coasts which seem to occupy similar roles in similar systems.

Figures 15 and 16 diagram the manner by which energy drains of stress, such as sharply fluctuating temperature, salinity and pollution wastes, channel energy into fewer species. When conditions are less stressed, energies of the food chains go into specialization and division of labor providing more zones, each occupied by a different species. Thus the less stressed estuaries of the northwest coast have more benthic clam types over the zones from fresh to salt water than at an equivalent latitude on the New England coast. More energy is available for the differentiation and organization that is necessary to prevent competitive exclusion.

Introduction of Faunas

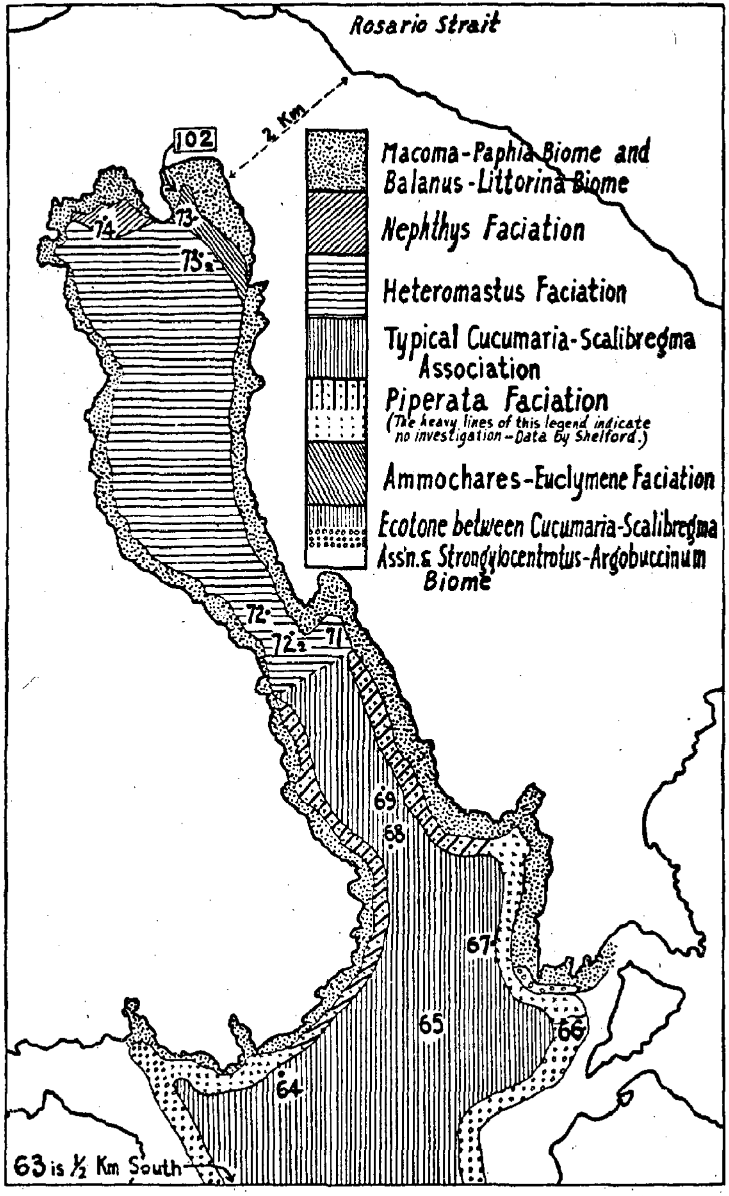
The introduction of faunas has been controversial in ecology. However, the experience of establishing the Japanese oyster in estuaries of the Pacific Northwest or exotic and fast-growing trees suggests that opportunities for developing improved yields to man may come from bringing in species less under local controls. On the other hand the fast spread of agricultural diseases, weeds and animal pests in American cities suggests dangers, cautions and difficulties of predicting outcome of transplants. According to Elton (1958) and many others, the fast spread of transplants in spectacular and permanently disrupting ways on big continents is associated mainly with areas already disturbed there. The transplants do not invade the well-established large systems, but enter the disturbed areas or the small or remote areas that may be regarded as missing major elements of possible support. In marine waters, ships and currents enable frequent introductions. With the development of more disturbed estuaries, more successful invaders may be expected as part of new designs for new conditions.

For those considering transplants or the dangers of introductions, the classification of estuaries may be useful in helping to indicate areas where analogs are to be found which may have adaptations to similar regimes.

Table 2. Examples of West and East Coast Niche Substitutions, Gulf Coast Equivalents and tropical types when stressed.

System Type	Description of Role	Tropical Stressed	Upper West Coast	Gulf Coast	Upper East Coast
Oligohaline river mouth	Clam with great capacity to burrow from cold and adapt to salinity variation		Mya arenaria	Rangia	Mya arenaria
	Oyster reef niche	Crassostrea virginica	Ostrea gigas	Crassostrea virginica	Crassostrea virginica
Middle salinity estuary	General crab carnivore, moving in and out of varying salinity	Callinectes	Dungeness crab Cancer	Blue Crab Callinectes	Green crab, Cancer
High salinity estuary	Top carnivore in bottom irregularities	Panulirus lobster	King crab Paralithodes	Stone crab Menippe	Homarus lobster
Kelp system	Algal forests, bottom attached seaward of surf	—	Macrocystis	—	Laminaria
Beach and surf zone	Deep digging clam adapted to heavy energies just seaward of breakers	Spisula	Razor clam Siliqua	Spisula	Spisula surf clam
	Surf zone sand dollar	Mellita	Dendraster	Mellita	Echinarachnius
Intertidal rocks*	Grazers of intertidal rocks, periwinkles	Littorina ziczac	Littorina planaxis Littorina scutellata	Littorina irrorata	Littorina litorea
	Intertidally protected filter feeders barnacles,	Balanus amphitrite	Gooseneck barnacle	Balanus eburneus	Balanus balanoides
	Ulva	Ulva	Ulva	Ulva	Ulva
Coastal Plankton	Zooplankton eater	Anchovy	Pacific herring, Sardines	Menhaden Threadfin	Atlantic herring Alewives

*Hedgepeth (1953, 1967)


Rosario Strait
2 Km
102
Macoma-Paphia Biome and Balanus-Littorina Biome
Nephthys Faciation
Heteromastus Faciation
Typical Cucumaria-Scalibregma Association
Piperata Faciation
(The heavy lines of this legend indicate no investigation—Data by Shelford.)
Ammochares-Euclymene Faciation
Ecotone between Cucumaria-Scalibregma Ass'n.& Strongylocentrotus-Argobuccinum Biome
74
73
73s
72
72s
71
69
68
67
66
65
64
63 is ½ Km South

Provisional map indicating the faciations of the Cucumaria-Scalibregma association (Pandora-Yoldia biome) in and adjacent to East Sound. Either a narrow strip of Macoma-Paphia biome, or the Pisaster ochraceus faciation of the Strongylocentrotus biome occurs between the Cucumaria-Scalibregma association (or its faciations) and mean low tide. The width of both of these is greatly exaggerated. The intertidal area is occupied locally by the Macoma-Paphia biome in its lower edge and by the Balanus-Littorina biome elsewhere. These details cannot be shown, to scale, on this map.

Fig. 15 . A north temperate estuary with relatively uniform salinity and temperature regimes allowing energies for differentiation of bottom subsystems. East Sound in Orcas Island, Puget Sound, Washington (Shelford et al., 1935).

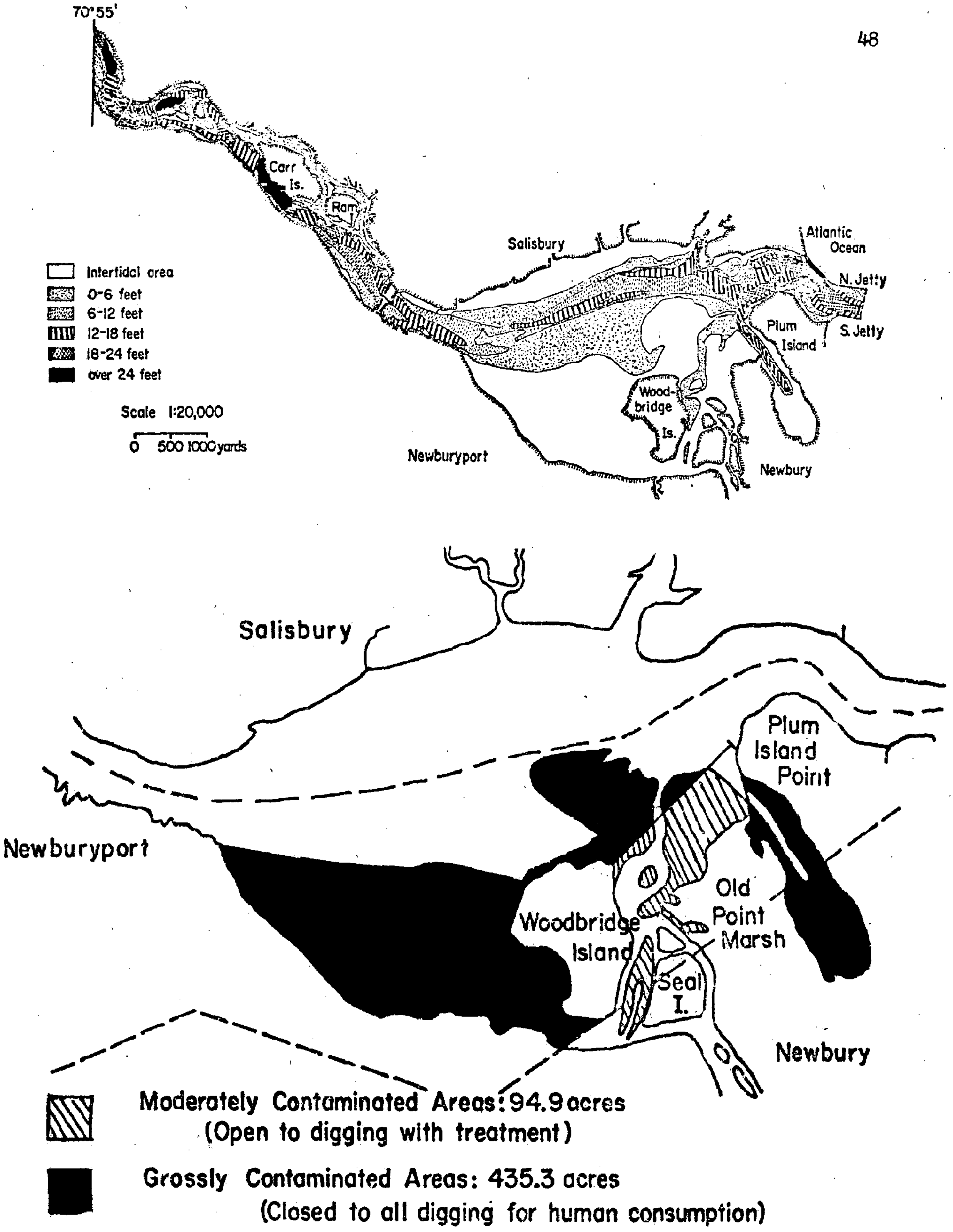

70°55'
Carr Is.
Ram I.
Salisbury
Atlantic Ocean
N. Jetty
S. Jetty
Plum Island
Wood-bridge Is.
Newburyport
Newbury
Intertidal area
0-6 feet
6-12 feet
12-18 feet
18-24 feet
over 24 feet
Scale 1:20,000
0 500 1000 yards
Salisbury
Newburyport
Plum Island Point
Old Point Marsh
Woodbridge Island
Seal I.
Newbury
Moderately Contaminated Areas: 94.9 acres
(Open to digging with treatment)
Grossly Contaminated Areas: 435.3 acres
(Closed to all digging for human consumption)

Fig. 16 . Merrimac Estuary, Mass., stressed by large temperature and salinity variations. The enlargement below shows soft shell clam beds which predominate (Jerome, Chesmore, Anderson, and Grice,1965)

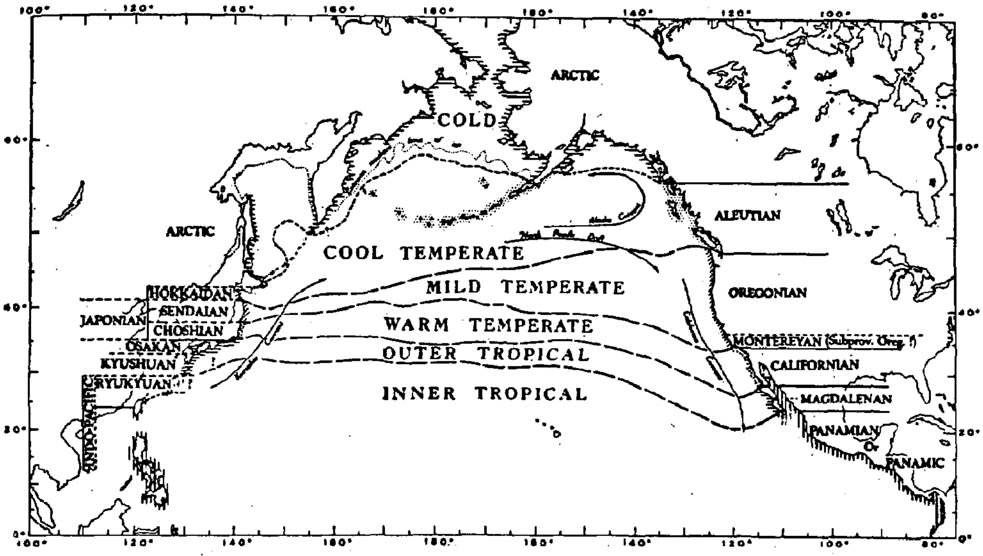
Species may be rapidly reprogrammed (physiologically, genetically, or by substitution of stocks) to time their energy demands and services to the system so as to maximize its own survival and its contribution to the system pattern's survival. Sakuda (1966b) in Figs. 12 and 13 shows for the oyster, Crassostrea virginica, different patterns of body thickness and reproductive activity in Hawaii as compared with more temperate latitudes.

The Historical Factor

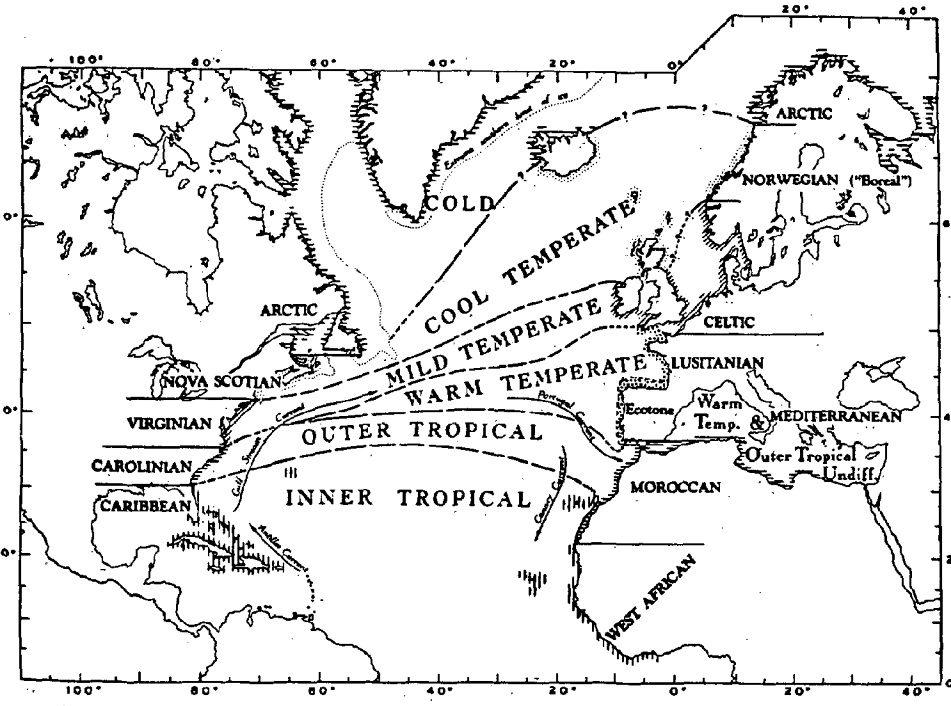
Deep divisions of opinion and belief exist among biologists considering the distribution of marine organisms and their ecosystems. Many biologists are concerned with long term evolution, speciation, and other historical events that have made available the present genetic material for ecosystems. Some believe that organisms live at a place if they can get there and if there is nothing toxic or lethal to them there. Being concerned with evolutionary pedigrees, these biologists consider one taxonomic group at a time and draw maps of distributions from which theories are derived regarding possible events which increased access, mechanisms isolating stocks long enough for genetic change, and other historical actions. These theories do not require of the organisms that they contribute closed loop work services, mineral cycling, economy of adaptations or other ecological performance criteria as a requirement for incorporation into a system. These approaches sometimes contrast with ecosystem theorists, starting with Darwin, who found the requirements of the system imposing choices on whatever genetic material was at hand to develop adaptations required for system survival. Surely both are necessary for the existence of an ecosystem: (a) the genetic information represented by the species, from which choices may be made and (b) the selective actions of organized system in loop rewarding those species which make service contributions that optimize the system's energy utilization and mineral cycles in work towards survival and continuation. With the strong energies of circulation in the sea, the historical factor may not be critical in limiting a system in any one place. The argument over the importance of historical access is involved in all plans for change as with the proposed Panama Sea level canal.

Biogeographic Classifications

Examples of the biogeographic province approach are given in Figs. 17 and 18. In Figure 17 are zones of similar temperature regimes to which many species are correlated because of their physiological adaptations for maintenance, enzyme operation, seasonal programming of reproduction , and common access to genetic pools. The ultimate reason for the correspondence of seasonal programming and temperature regimes may be that both are a function of the energy input program from the sun and other sources. The seasonal energy pulse moves through the compartments of the food chain as heat energy accumulates in the water. Similar light energy regimes tend to develop with similar temperature regimes. In Fig.18A are calculations of similarity with latitudinal zones on the west coast by North and Hubbs (1968). Biogeographic provinces are also shown as classified by those studying animal distribution on the west coast without regard to the systems the animals are serving. Although discontinuous patterns in faunal lists are found when sharp changes in temperature occur on some capes such

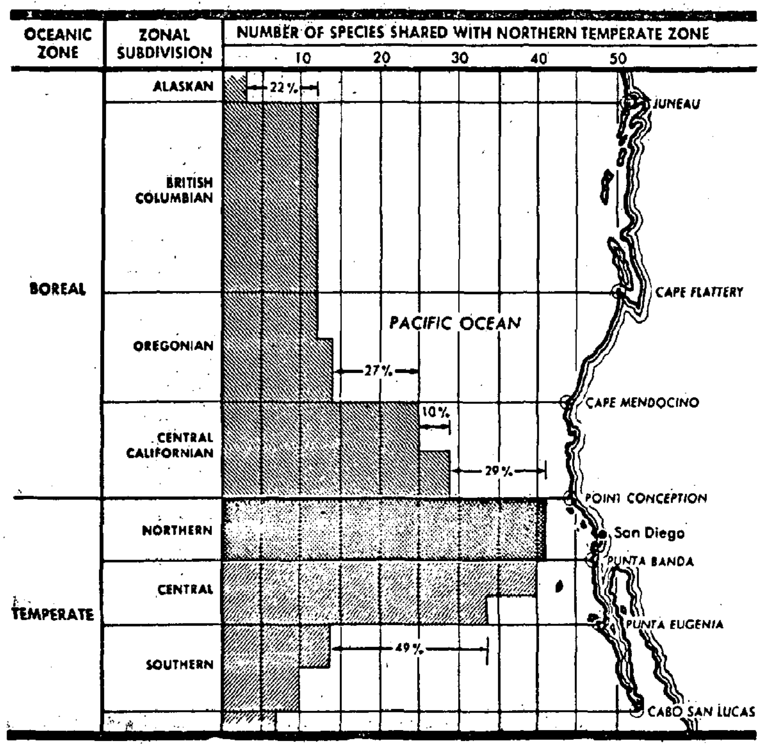

100°
120°
140°
160°
180°
160°
140°
120°
100°
80°
60°
40°
20°
0°
ARCTIC
COLD
ARCTIC
COOL TEMPERATE
MILD TEMPERATE
WARM TEMPERATE
OUTER TROPICAL
INNER TROPICAL
HOKKAIDAN
SENDAIAN
JAPONIAN
CHOSHIAN
OSAKAN
KYUSHUAN
RYUKYUAN
ALEUTIAN
OREGONIAN
MONTEREYAN (Subprov. Oreg. ?)
CALIFORNIAN
MAGDALENAN
PANAMIAN
Or
PANAMIC

Pacific molluscan provinces and subprovinces; the northern boundaries mark the northern latitudinal limits of a significant number of species. Marine climates, based on the duration of marine temperatures at the limits of molluscan species. Base map from U. S. Navy's *Marine Climatic Atlas of the World.*


100°
80°
60°
40°
20°
0°
20°
40°
60°
40°
20°
0°
ARCTIC
NORWEGIAN ("Boreal")
COLD
COOL TEMPERATE?
MILD TEMPERATE
WARM TEMPERATE
OUTER TROPICAL
INNER TROPICAL
ARCTIC
NOVA SCOTIAN
VIRGINIAN
CAROLINIAN
CARIBBEAN
CELTIC
LUSITANIAN
Ecotone
Warm Temp. &
MEDITERRANEAN
Outer Tropical
Undiff.
MOROCCAN
WEST AFRICAN
Gulf Stream
Canary Current
Portugal
Antilles C.

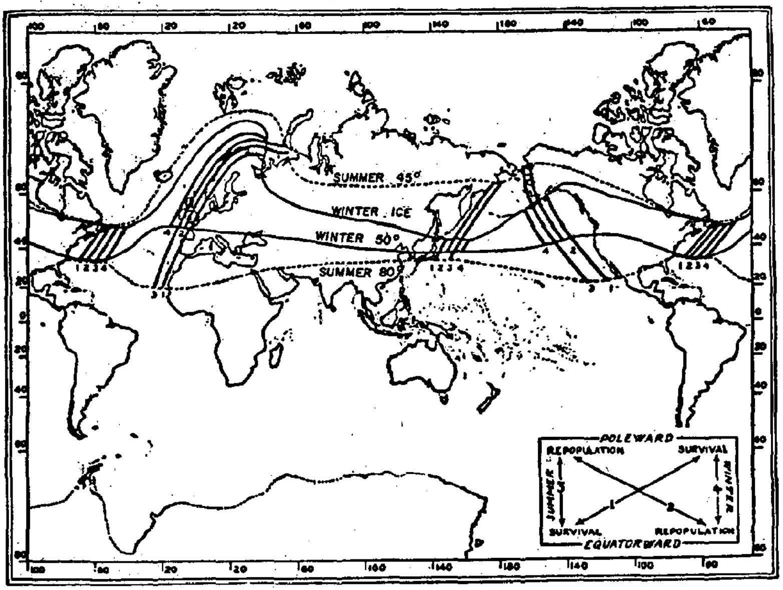
Atlantic molluscan provinces and subprovince; the northern boundaries mark the northern latitudinal limits of a significant number of species. Marine climates, based on the duration of marine temperatures at the limits of molluscan species. Base map from U. S. Navy's *Marine Climatic Atlas of the World.*

Fig. 17. Biogeographic provinces related to temperature regimes and faunal similarities (Hall, 1964).



Decline in affinity with the San Diego fauna as a function of distances. Boreal and temperate zones after Hedgpeth (1957), with Point Conception taken as the boundary. The zonal subdivisions are mainly for discussion purposes and may or may not be of zoogeographic importance.

Fig. 18A. Biogeographic provinces on the U.S. west coast with affinity calculations (North and Hubbs, 1968).


SUMMER 45°
WINTER ICE
WINTER 50°
SUMMER 80°
1 2 3 4
POLEWARD
REPOPULATION
SURVIVAL
SUMMER
WINTER
1
2
3
4
SURVIVAL
REPOPULATION
EQUATORWARD
180
140
100
60

Four zonal types of distribution

Extent of the four major zonal types based on the mean temperatures at Newfoundland and Cape Hatteras as limiting intensities (from Hutchins, 1947).

Fig. 18B. World temperature regimes (from Hedgepeth, 1957).

as Cape Cod or Cape Hatteras, the ecosystems may be continous with little change in general character because of niche substitutions. The boundaries of biogeographic provinces thus do not correspond with boundaries for ecosystem types and thus may not provide a basis for management. Species adapted to the more severely stressed conditions tend to be world wide and less related to biogeographic provinces. Heald (1968) in providing approximate maps for fisheries (shellfish included) finds patches and zones rather than continuous distributions corresponding to biogeographic provinces. Ecological differentiation determines the systems rather than the factors of access and temperature.

Arctic Systems

As one moves north, and the pulse of temperature and photosynthesis gets more and more extreme, the properties of temperate zones of the main coasts of the United States retain much of their character with some variations and species substitutions. Entirely different systems appear with the presence of ice as glaciers, as glacial melt patterns, as sea ice stress and in systems that are actually in and on the ice. The combination of extreme tides and extreme cold increases intertidal stress on mud flats beyond that capable of supporting temperate types of systems. In our classification we identify as Arctic only those systems not recognizable in the temperate latitudes.

Tropical Systems

Although stressed systems are similar in temperate and tropical versions, systems not exposed to sharp stress are characteristically different from those of temperate latitudes, with species that have neither low temperature adaptations or adaptations for sharp seasonal changes. Thus the coral reefs, tropical plankton waters, and oceanic mangroves (in areas of small tidal range) have long been recognized as types of maximum diversity and beauty, of maximum aesthetic value. A system is characterized as tropical when it is associated with stable conditions, generates high diversity and does not occur in areas subjected to frost.

Diversity of Contributing Subsystems in Large Waters

When salinities and temperatures have only moderate ranges, when other energy stress drains are small, and when the system size is large, the division of specialization is not only by inclusion of many species, but sub-systems of relatively low diversity are developed that provide a pattern of alternating diversity much in the way that a country-side is dispersed with cities of different main contribution to the overall economy. It is important to an understanding of the estuarine systems to define both the subsystems and the overall system as well. Thus the bottoms of high salinity stable bays are divided up into subsystems of benthic clams and worms, each being dominated by some associations while the overall bay system _in toto_ has a large diversity of specialists contributing to the pools of mineral nutrients and plankton operators. Examples are the patterns of bottom associations on the continental shelves as reported in extensive studies by Zenkevich (1963).

The patterns of alternating subsystems in benthic fauna is found in estuarine regions in the higher salinity bays and archipelagos as with the example of

Mercenaria clam beds off Massachusetts in Fig. 19 (Ropes and Martin, 1960). The specialization of beds of different species, which all contribute to the single system of water, mineral cycling and plankton drifting by, is another example of the division of niches possible when stress is less and there is high diversity of large animals, distance, temporal programming, channeled mineral flows and other organizational mechanisms preventing competitive exclusions that might otherwise develop.

ECOLOGICAL SYSTEM TYPES IN THE CLASSIFICATION

The proposed classification of coastal systems is given in Table 1. It was derived from considerations of energy inflow, stress and diversity development plus a lot of intuition and suggestions of our many discussants. The names used for each system are not really important, except that we have sought common words in their regular English usage, selected to suggest the features of characteristic energy flows responsible for our recognition of the type. For clarification, column 2 of Table 1 lists the energy source or energy stress which is characteristic. Following Table 1 is a consideration of the basis for the recognition of each type.

Indicator Species in Stressed Systems

In highly diversified systems such as the near-shore shelf waters no one species is a system indicator because with slightly different conditions, a different species is tuned to take over local dominance. In the stressed environments and those requiring much programmatic adaptation species are few and those present are so highly adaptive that their presence identifies the nature of the regime. Bottom animals have proven useful as indicators of systems as shown by Parker (1959) in Fig. 20. The extensive efforts to use foraminifera for this purpose is the subject of Part II. Jeffries (1962b) using Raritan Bay, New Jersey summarizes use of 8 calanoid copepods as marker of steady injection of coastal plankton into systems characterized by mixing.

Salinity Adaptations

Salinity adaptations apparently require considerable energies, not so much in the actual operation but in the carrying of the physiological machinery and programs of response to salinity fluctuations.

In Figs. 21-25 are some salinity ranges for which certain species are adapted. Under these conditions they substitute in the niches for similar species which are adapted for other ranges. The adaptations are not only to the salinity level but to the range of fluctuation. Sloan found very high diversities in regular estuarine salinity ranges where the water was steady because of its source in salty springs, as contrasted with low diversities in tidal estuaries where salinities are continually fluctuating daily and seasonally. The fairly low diversities in the estuarine waters at the mouth of Lake Maricaibo, Venezuela (Fig.22) contrast with the high diversities in waters at the same latitude not exposed to continual salinity shocks. Sanders, Mangelsdorf and Hampton (1965) showed in the Pocasset River estuary that the infauna in more stable salinity was diverse, while the fauna more exposed to the shifting salinities in the waters above were few in species (Fig. 25).

These examples and others cited in the chapters that follow emphasize the importance of the fluctuation of properties in diverting energies from other potentials.

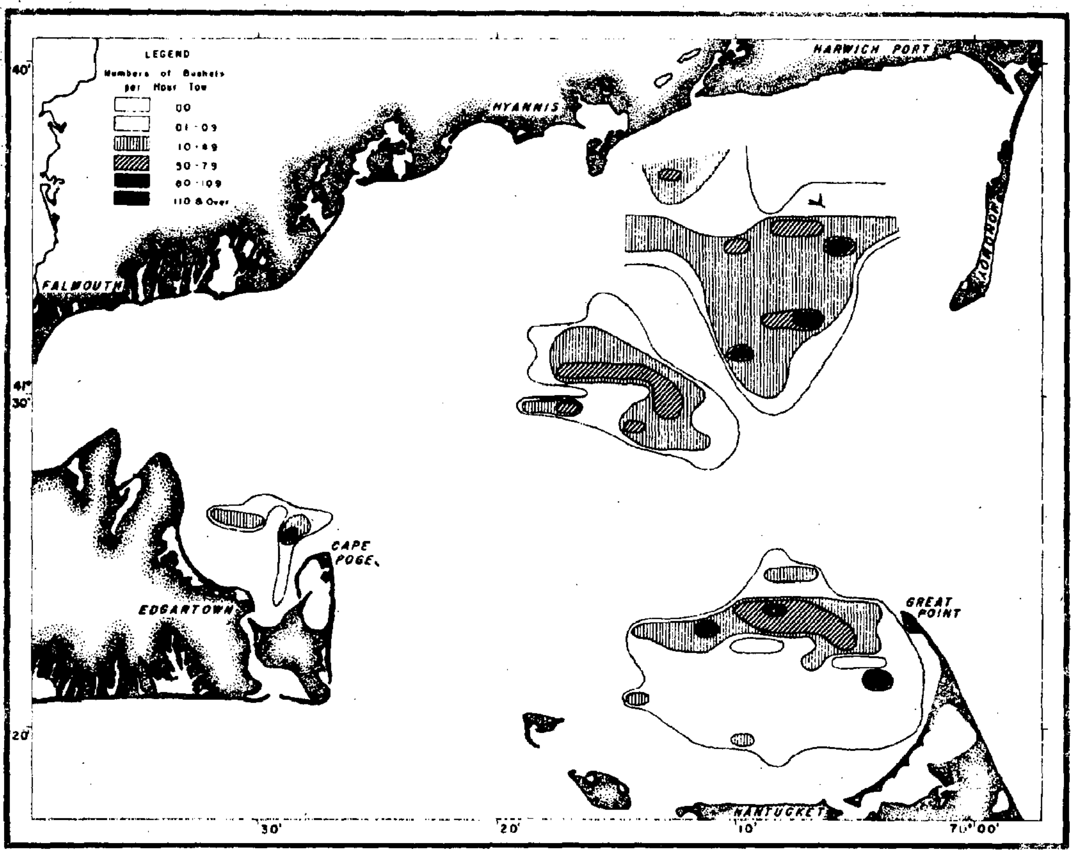
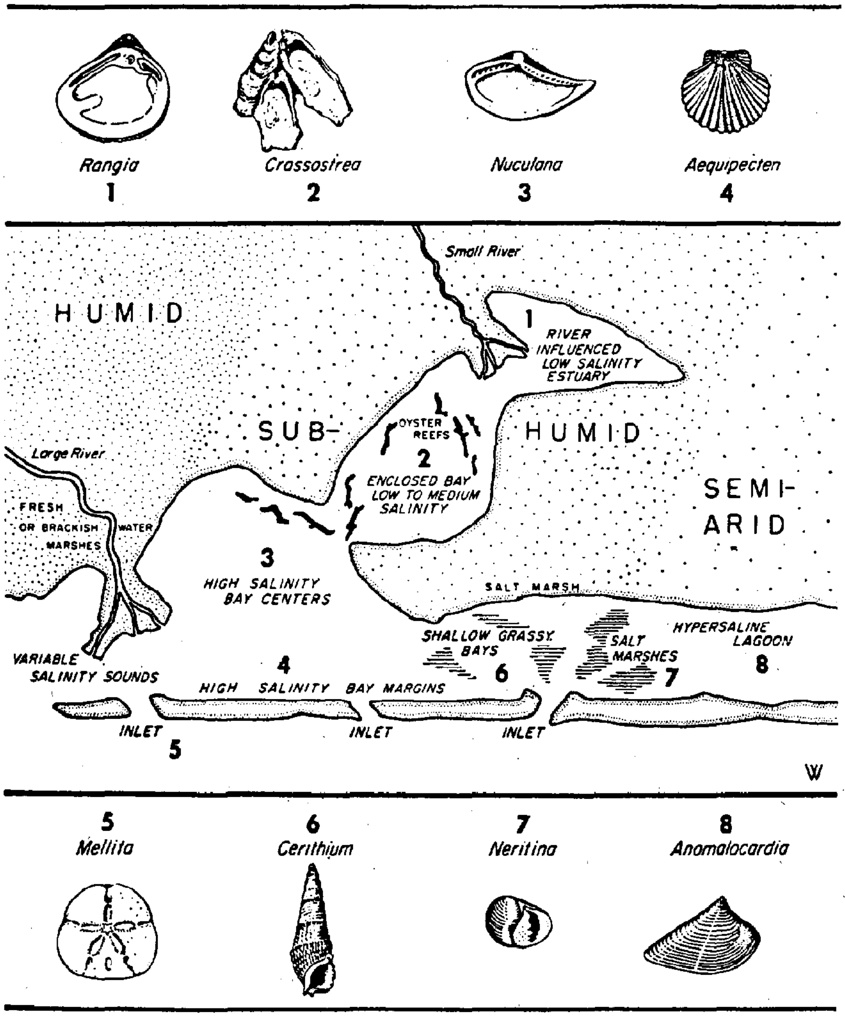

LEGEND
Numbers of Bushels per Hour Tow
00
01 - 09
10 - 49
50 - 79
80 - 109
110 & Over
40'
41°
30'
20'
30'
20'
10'
70°00'
FALMOUTH
HYANNIS
HARWICH PORT
MONOMOY
CAPE POGE
EDGARTOWN
GREAT POINT
NANTUCKET

Fig. 19 Hard shell clam (Mercenaria mercenaria) abundance (bushels per 1-hour tow) in Nantucket Sound, Massachusetts (From Ropes and Martin 1960; Fig 5).

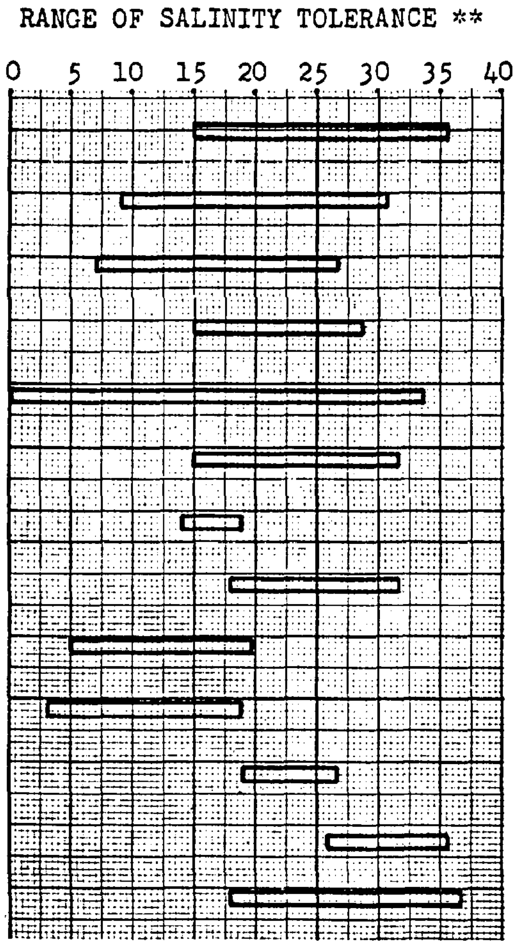

Rangia
1
Crassostrea
2
Nuculana
3
Aequipecten
4
Small River
HUMID
1
RIVER INFLUENCED LOW SALINITY ESTUARY
OYSTER REEFS
2
ENCLOSED BAY LOW TO MEDIUM SALINITY
SUB-HUMID
SEMI-ARID
Large River
FRESH OR BRACKISH WATER MARSHES
3
HIGH SALINITY BAY CENTERS
SALT MARSH
SHALLOW GRASSY BAYS
6
SALT MARSHES
7
HYPERSALINE LAGOON
8
VARIABLE SALINITY SOUNDS
4
HIGH SALINITY BAY MARGINS
INLET
5
INLET
INLET
W
5
Mellita
6
Cerithium
7
Neritina
8
Anomalocardia

Diagrammatic representation of bay and lagoonal macro-invertebrate environments in relation to general climatic provinces. Figured species is not everywhere found in the Texas region, but represents genus found in these environments throughout North America. *Rangia* (1) also found at Delta shores and distributaries of large rivers. *Nuculana* (3) also common in variable salinity sounds and pro-delta slopes. *Mellita* (5) migrates through inlets into bays. Certain species of *Neritina* (7) also found in fresh- or brackish-water marshes near large river mouths.

Fig. 20. Indicator bottom animals in ecosystem types of the Gulf of Mexico (Parker, 1959). 1 and 7, oligohaline system; 2, oyster reef; 3, medium salinity plankton system; 4 and 6, shallow bottom vegetation system; 7, salt marsh; 8, hypersaline lagoon.

SALINITY TOLERANCES OF SOME INVERTEBRATES OCCURRING WITHIN THE DELAWARE RIVER ESTUARY (compiled from several sources)

*	ORGANISMS
(1)	Cliona celata (boring sponge)
(2)	Nereis succinea *** (a clamworm)
(1)	Crassostrea virginica **** (Atlantic oyster)
(3)	Urosalpinx cinerea ***** (oyster drill)
(1)	Callinectes sapidus (blue crab)
(4)	Neopanope texana sayi (Say's mud crab)
(5)	Panopeus herbsti (a mud crab)
(4)	Hexapanopeus angustifrons (a mud crab)
(5)	Eurypanopeus depressus (flat mud crab)
(5)	Rhithropanopeus harrisi (brackish water mud crab)
(2)	Aeginella longicornis (long-horned caprellid)
(1,6)	Loligo pealii (common squid)
(1)	Lolliguncula brevis (short squid)



* Sources: (1) Spector, 1956; (2) Amos, 1954 and unpublished data; (3) Carriker, 1955; (4) Cowles, 1930; (5) Ryan, 1956, and (6) Haefner, 1959.

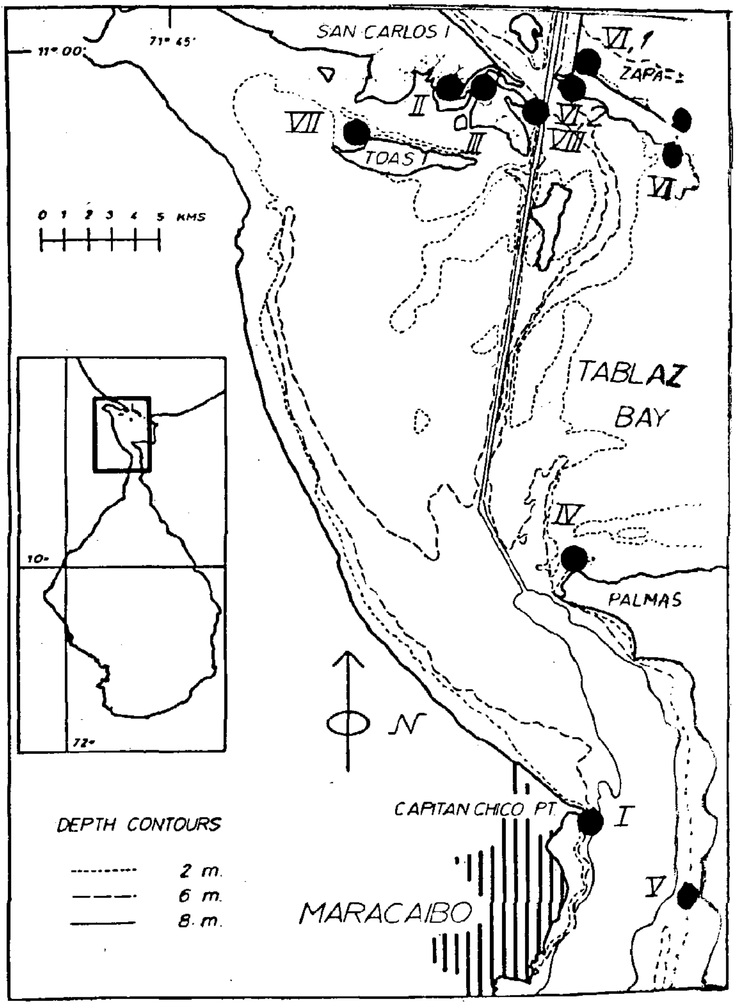
** Stauber (1943) pointed out, in discussing a graphic method of representing salinity condition in Delaware Bay, that species are limited to certain regions of the estuary by the effects of the extremes in the salinity range and of their duration rather than by the average conditions. For a further discussion of tolerances see Fry (1947).

*** At summer temperatures (20-27°C).

**** Can withstand short-time salinity changes of 0-42 $^{o}/oo$ in the laboratory (1).

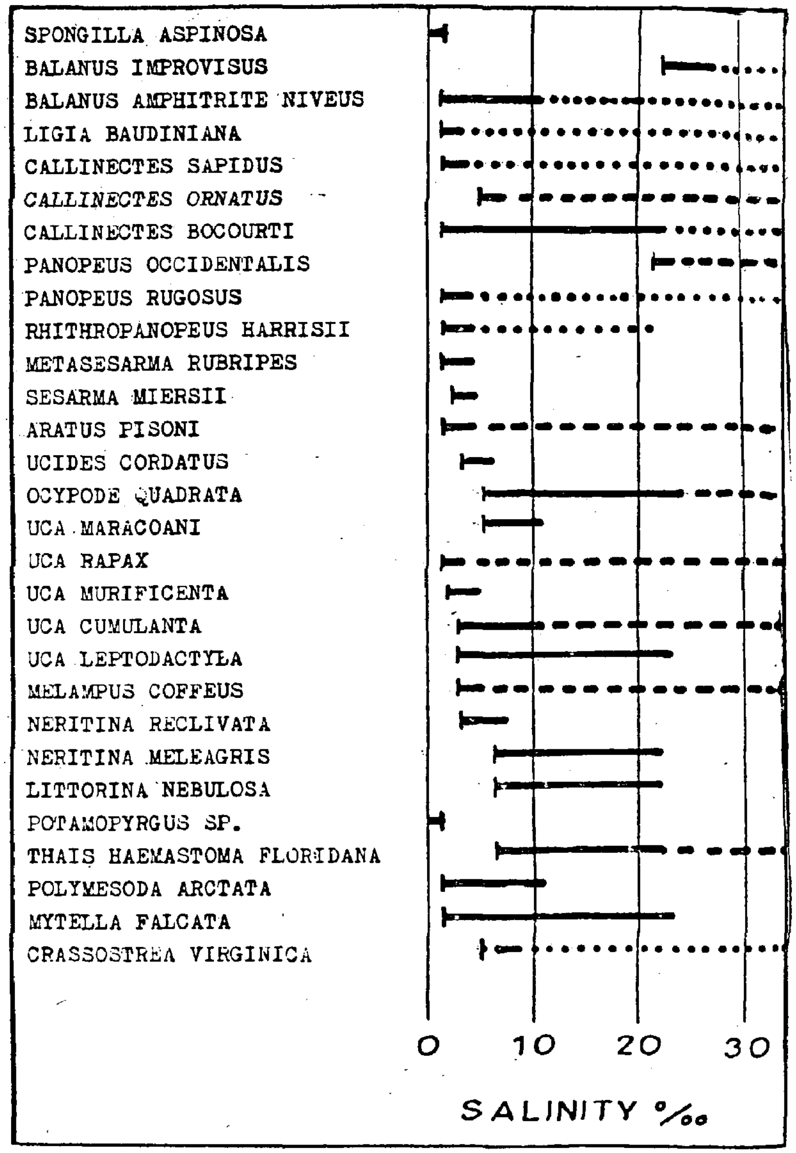
***** Can survive salinities as low as 8 $^{o}/oo$ during the winter (2).

Fig. 21. Salinity adaptations of estuarine animals in a temperate area (Shuster, 1959).


SAN CARLOS I
ZAPARA
TOAS I
TABLAZ BAY
PALMAS
CAPITAN CHICO PT
MARACAIBO
I
II
III
IV
V
VI
VI, 1
VI, 2
VII
VIII
11° 00'
71° 45'
10°
72°
0 1 2 3 4 5 KMS
N
DEPTH CONTOURS
2 m.
6 m.
8 m.

Map of the northern portion of Lake Maracaibo

Fig. 22. Salinity adaptations of estuarine animals in a tropical estuary, Lake Maracaibo, Venezuela (Rodriguez, 1963).



Salinity ranges of the invertebrates found in the estuary.

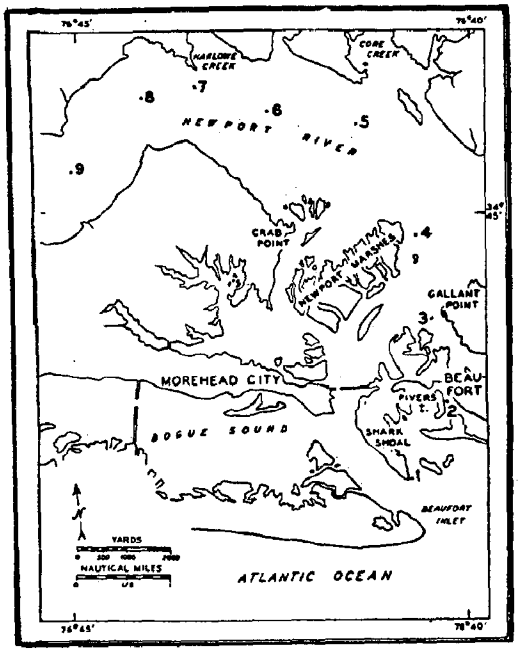
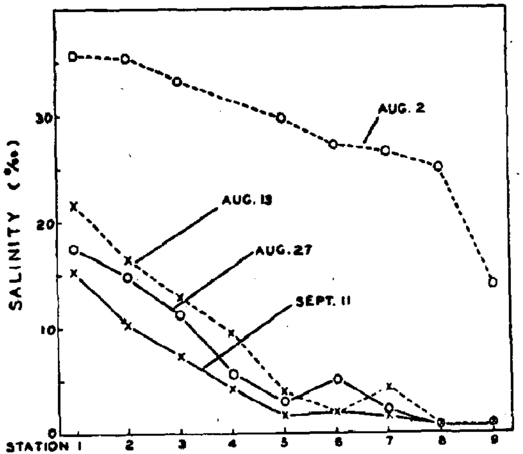

76°45'
76°40'
34°45'
HARLOWE CREEK
CORE CREEK
.8
.7
.6
.5
.9
.4
3
2
NEWPORT RIVER
CRAB POINT
NEWPORT MARSHES
GALLANT POINT
MOREHEAD CITY
BEAUFORT
PIVERS I.
SHARK SHOAL
BOGUE SOUND
BEAUFORT INLET
N
YARDS
NAUTICAL MILES
ATLANTIC OCEAN

Chart of the Beaufort (N. C.) area showing location of hydrographic stations: 1—Shark Shoal, Pivers I., 3—Gallant Point, 4—Newport Marsh, 5—b Point, 6—Midway, 7—White Rock, 8—Turtle Rock, Cross Rock.



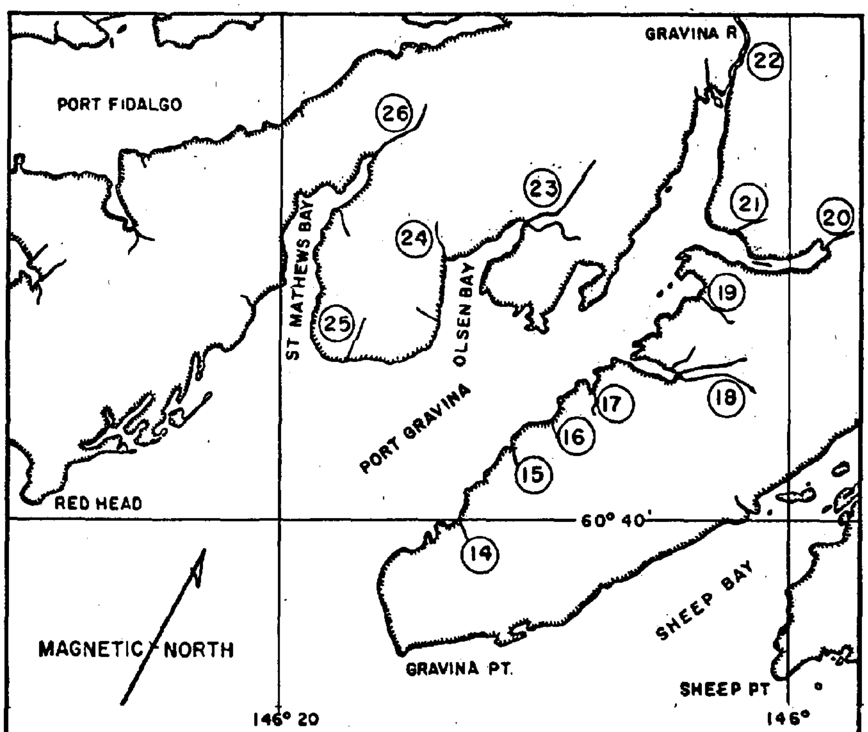
Salinity profiles, August 2, 13, 27, and September 11, Newport River, 1955. (Hurricane Connie passed on August 12, and Diane, on August 17.)

Conditions and results of salinity tolerance experiments.

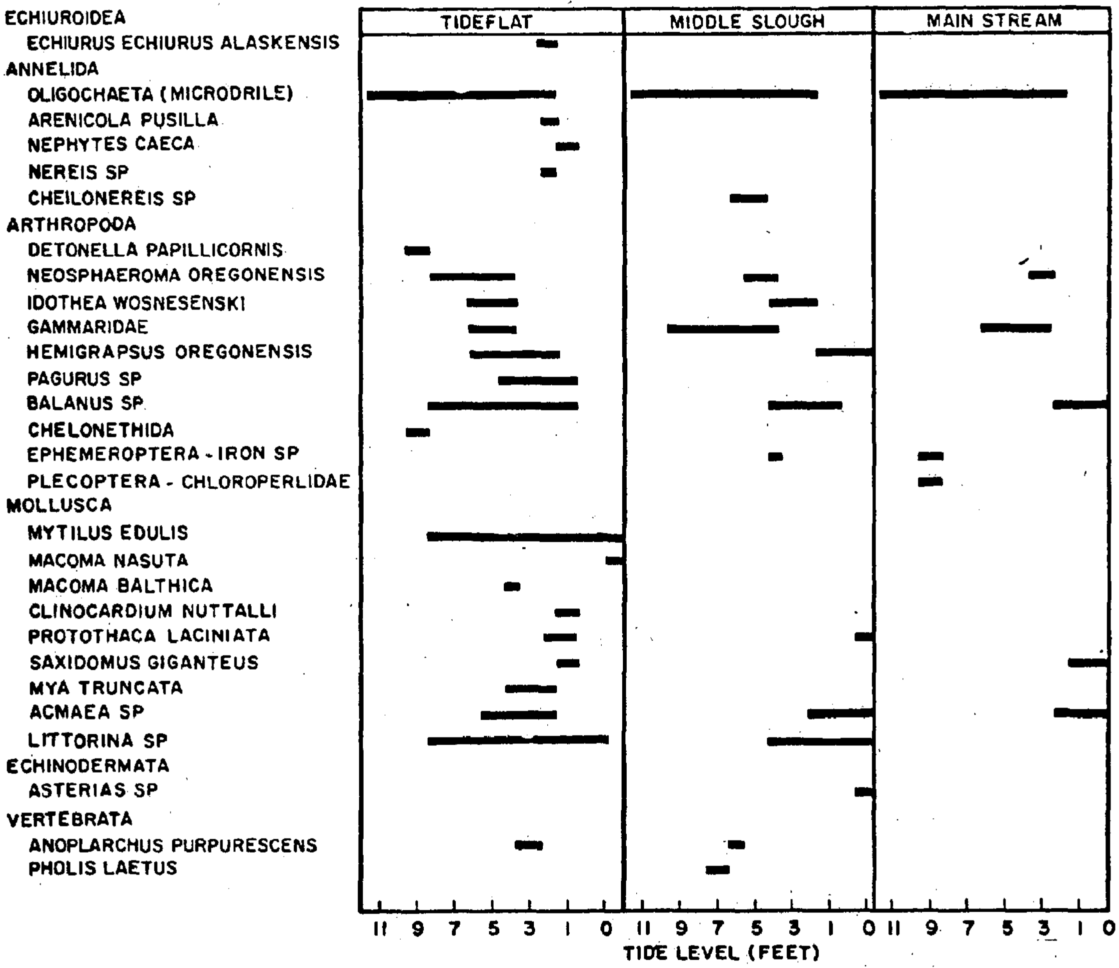
Species	Length range (mm)	Number per salinity interval	Temperature range (°C)	Salinity Death Point (o/oo)
Gastropods:				
Nassarius vibex	11-17	13	22.8-26.2	9
Thais floridana	47-78	4	28.0-28.5	9
Odostomia impressa	1-4	20	28.0-30.0	11
Urosalpinx cinerea	12-30	20	26.1-28.1	11
Busycon carica	41-86	4	26.0-26.5	11
Cerithium floridanum	24-48	6	26.0-26.5	13
Fasciolaria hunteria	38-91	3	27.5-28.5	17
Cantharus tinctus	15-30	16	26.5-27.0	18
Thais veligers	—	50	25.0-27.5	9
Cerithium veligers	—	30-70	23.5-26.0	21
Pelecypods:				
Mercenaria mercenaria	30-123	4	25.3-27.5	(0)
Modiolus demissus	62-98	6	28.2-28.9	5
Crassostrea virginica	20-117	6	26.0-28.0	7
Brachidontes exustus	8-22	25	24.5-27.5	13
Chione cancellata	18-40	11	27.0-28.5	19
Decapods:				
Panopeus herbsti	20-40	4	24.0-27.5	3
Eurypanopeus depressus	4-17	11	25.0-27.5	3
Clibanarius vittatus	—	2	26.0-26.5	5
Pagurus longicarpus	—	18	22.8-26.2	9
Echinoderms:				
Asterias forbesi	55-120	4*	23.5-26.0	17
Arbacia punctulata	47	2	27.5-28.7	19
Lytechinus variegatus	48	1	27.5-28.7	23

* 10 specimens in 14, 16, and 18 o/oo dilutions.

Fig. 23A Salinity tolerances in the field and laboratory at Beaufort, North Carolina (Wells, 1961).

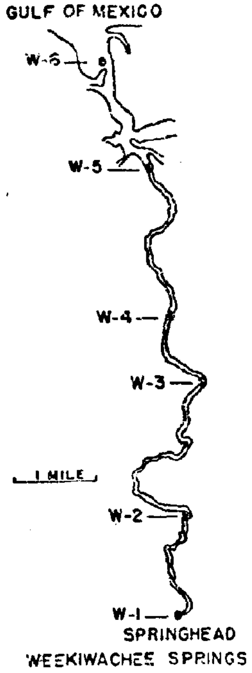

PORT FIDALGO
GRAVINA R
26
22
23
21
20
24
19
25
ST MATHEWS BAY
OLSEN BAY
PORT GRAVINA
17
18
16
15
RED HEAD
60° 40'
14
MAGNETIC NORTH
SHEEP BAY
GRAVINA PT.
SHEEP PT
146° 20
146°

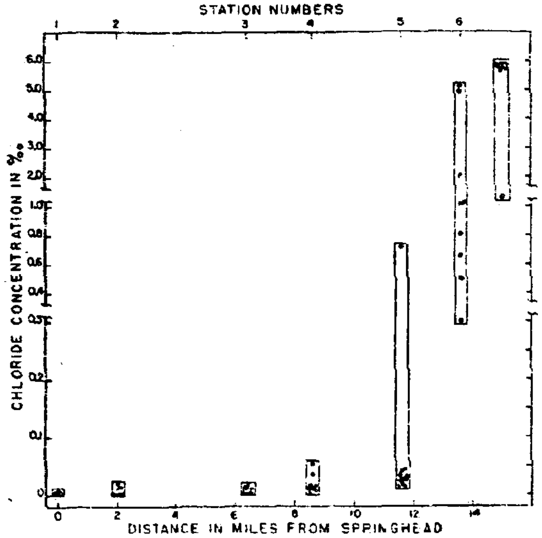
-Location and U.S. Fish and Wildlife Service reference number of spawning streams in Port Gravina, Prince William Sound.



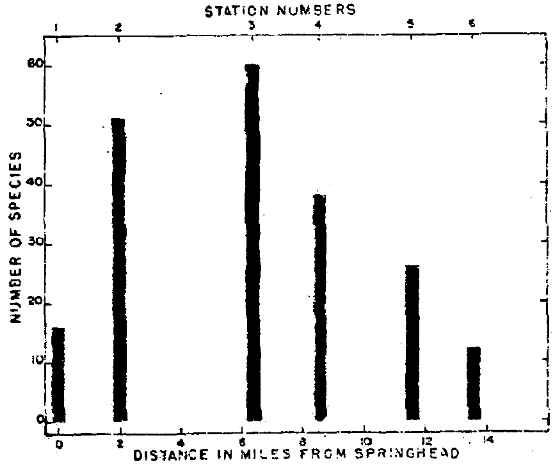
--Distribution of organisms by tide level, Olsen Creek drainage, 1961.

Fig. 23B. Adaptations to tidal position and salinity range in Alaska (Helle, Williamson, and Barcly, 1964).

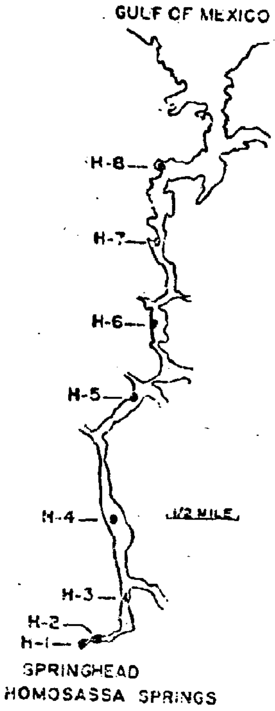

GULF OF MEXICO
W-6
W-5
W-4
W-3
1 MILE
W-2
W-1
SPRINGHEAD
WEEKIWACHEE SPRINGS

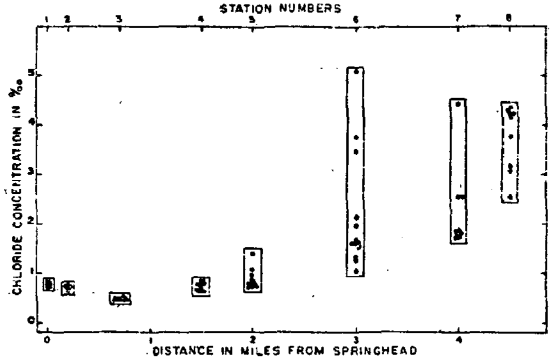


Chloride values in Weekiwachee Springs.

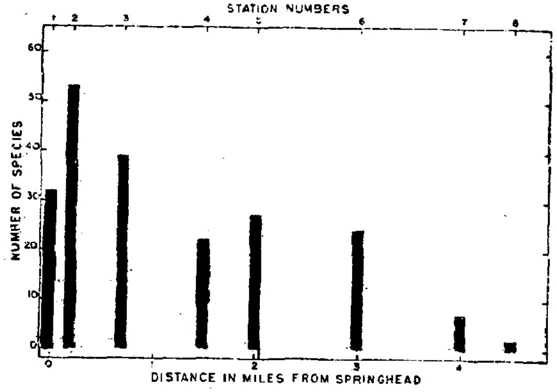


Numbers of insect species taken from collecting stations in Weekiwachee Springs.


GULF OF MEXICO
H-8
H-7
H-6
H-5
H-4
1/2 MILE
H-3
H-2
H-1
SPRINGHEAD
HOMOSASSA SPRINGS

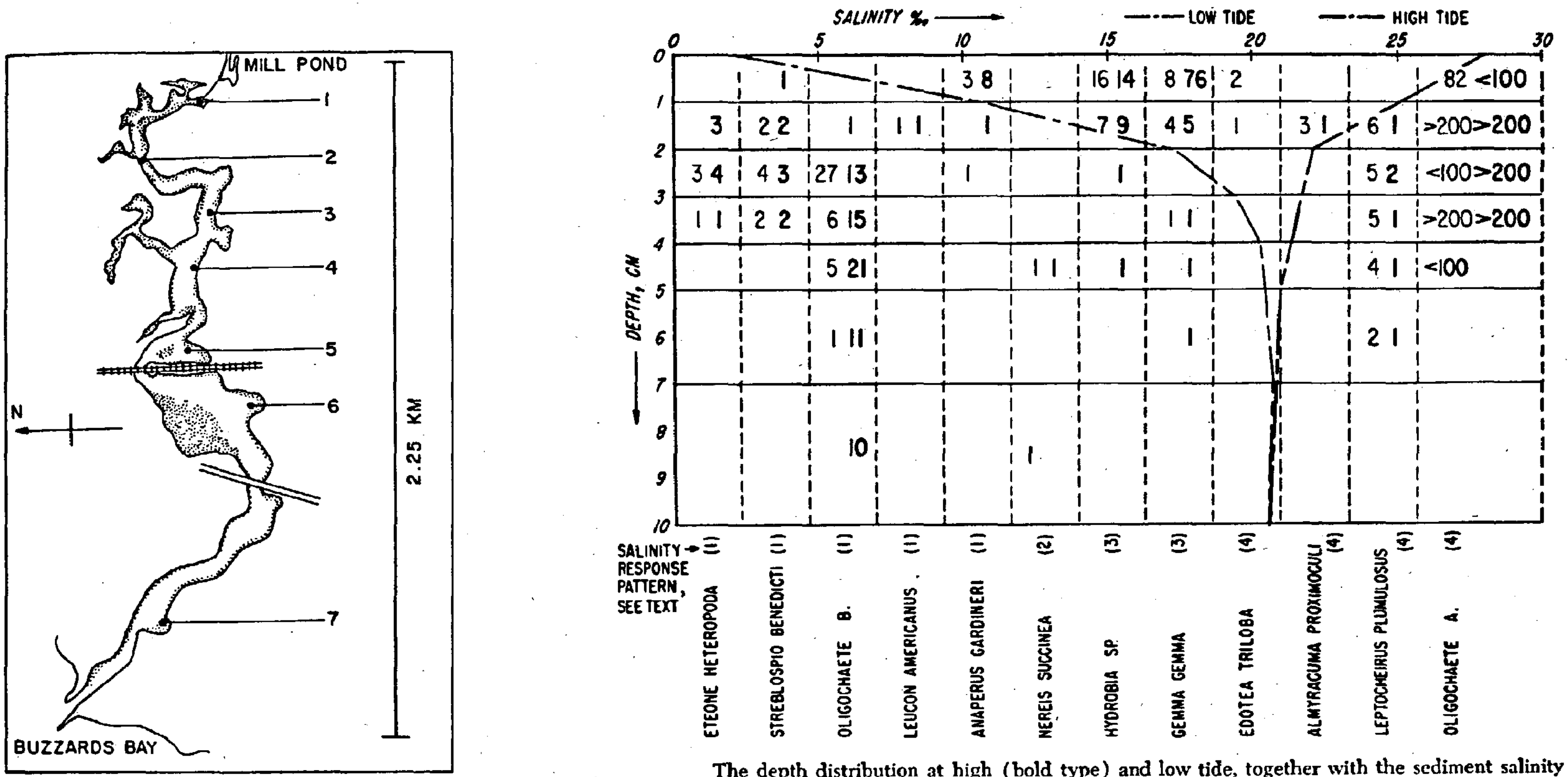


Chloride values in Homosassa Springs.



Numbers of insect species taken from collecting stations in Homosassa Springs.

Fig. 24. High species diversities in oligonaline salinities when they are steady as in Homosassa Spring, Florida (Sloan, 1956). Also shown in a freshwater spring in similar situation a few miles away. Faunas of both are mixed marine and freshwater origin.



Pocasset River

The depth distribution at high (bold type) and low tide, together with the sediment salinity at high and low tide and salinity response patterns of 12 benthic species at Station 3. A brown turbellarion is incorrectly labeled *Anaperus gardineri*. The animal found is definitely not *A. gardineri*.

Fig. 25 . Distribution of diversity with depth in the mud in an estuary in Massachusetts (Sanders, Mangelsdorf and Hampson, 1965). The waters above fluctuate sharply in salinity.

A. Naturally Stressed Systems of Wide Latitudinal Range

First consider those types of systems which are mainly organized around high energy stresses and which have less adaptations with latitude as discussed in the theoretical section. By and large these types are more difficult to injure permanently because their structure is already adapted to energy stress and the high energies serve to disperse and process wastes.

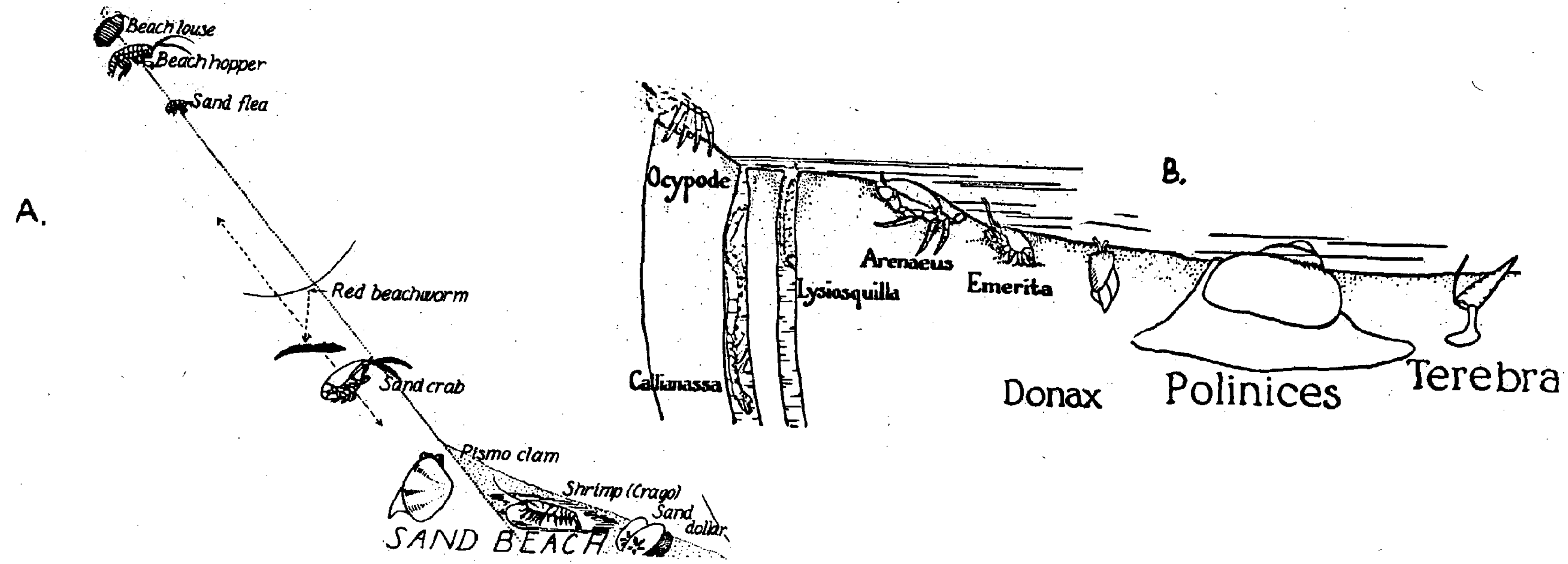
Rocky Sea Front (A-1)

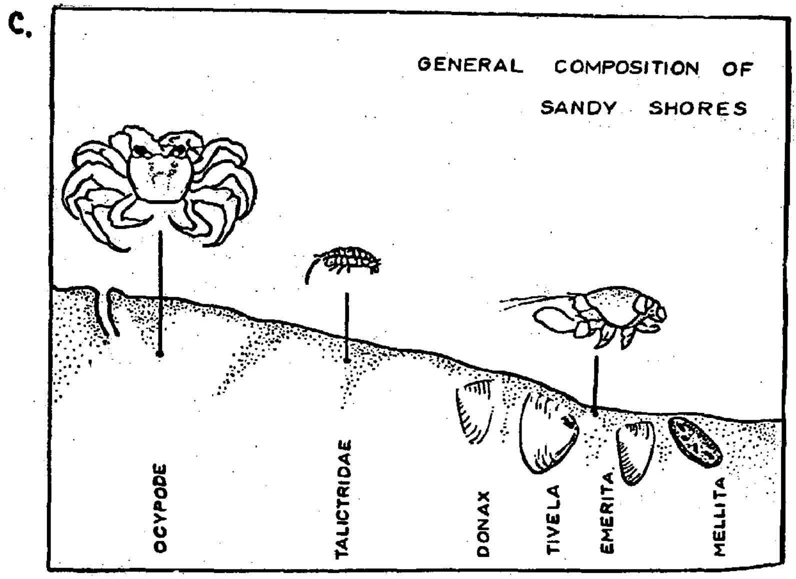
Rocky sea fronts occur on east and west coasts, Alaska, and Hawaii where glacial action, lava flows, or other geological action has left hard bare rocks at the shore receiving the pounding of open surf. In more northern latitudes rocky fronts are more important because of the scouring of glacial ice in earlier times and partly because of heavy wave energies that winnow away the deposit of beach sands. Because of the great range of tides in the north temperate zones, breaking waves cover a broader zone, and in northern climates summer heating stress is less on these rocks. For these reasons the characteristic distribution of algae and attached animals is better developed. With the sharp pulse of the season, surviving populations develop storage in animal and plant masses that last several years. The heavy brown algae carry on photosynthetic food making while exposed in air as well as in water. The mussels by their filter feeding of microscopic matter collect and mineralize plankton and detritus, releasing inorganic nutrients among the mats of algae. The algal production in turn is released back to the waters supporting plankton. Thus, the intertidal system is coupled to the estuarine waters, being a subsystem of the latter. Because of the recession of the tides, many kinds of marine grazers and carnivores are limited in access and large stocks of mussels and brown algae coat the rocks.

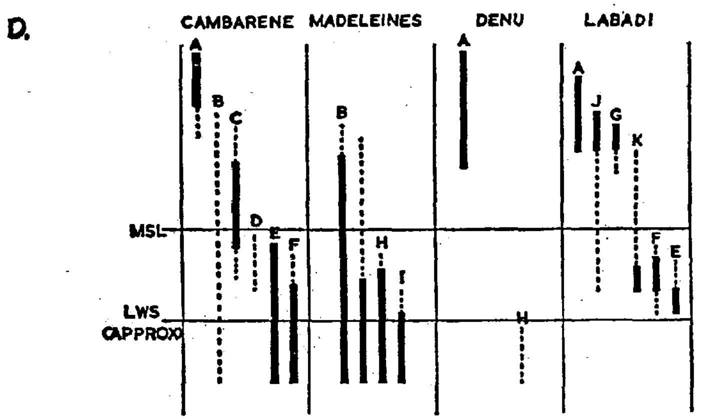
Although best developed on the rocks of Maine or Southern Alaska the system of algae and attached filter feeding animals is also found on rocks where they occur in jetties in Gulf States and on lava flows in heavy surf of Hawaii. In southern latitudes, the seasonal pulse and stress is less, tides are less and intertidal heating is greater. Animals have more rapid turnovers and are generally smaller and have less storage as related to seasonality.

High Energy Beaches (A-2)

South of Cape Cod on the east or Puget Sound on the west, sandy beaches become the most common coastal system on the front shoreline which receives breaking waves. Sand grain sizes are self-organizing in dependance on the energy of the waves. Surging waters are received, filtered, and returned to the sea. Very characteristic burrowing *Hippa* crabs, *Donax* clams and interstitial cosmopolitan beach fauna participate in the massive sand filter in the process of filtering organic matter. The beach line provides organization to passing water masses and serves many reproductive cycles in which eggs are deposited at the beach. The characteristic long shore current supports many migrations. The sand may be quartz-dominated along the main continent, of dark volcanic minerals near lava flows, or calcareous where terrigenous supply is low and available hard matter is from coral reefs or other calcareous substrates that increase towards the tropics. High energy beach systems are similar at all latitudes (compare animals in beaches from different latitudes in Fig. 26), but there are


A.
Beach louse
Beach hopper
Sand flea
Red beachworm
Sand crab
Pismo clam
Shrimp (Crago)
Sand dollar
SAND BEACH
B.
Ocypode
Callianassa
Lysiosquilla
Arenaeus
Emerita
Donax
Polinices
Terebra


C.
GENERAL COMPOSITION OF SANDY SHORES
OCYPODE
TALICTRIDAE
DONAX
TIVELA
EMERITA
MELLITA



–Diagrammatic comparison of zonation on sandy beaches at two localities in Ghana (Denu, Labadi) after Gauld and Buchanan (1956) and two (Cambérène, Madeleines) in Senegal after Sourie (1957). A, ocypods; B, *Ter* *micans*; C, *Nerine agilis*; D, *Glycera convoluta*; E, *Hippa cubensis*; F, *Donax* (?) *lchellus*; G, *Nerine cirratulus*; H, *Donax rugosus*; I, *Lumbrineris impatiens*; J, *Excirolana latipes*; K, *Urothöe grinaldi*.

Fig. 26. Similarities in faunas of temperate beaches(A and B) and high energy beaches of tropical areas(C and D).

A, California (Hedgepeth, 1967b; B, North Carolina (Pearse, Humm, and Wharton, 1942).
C, Venezuela (Rodriguez, 1959); D, Africa (Lawson, 1966).

variations. At the northern boundaries of the United States and southern Canada and Alaska, the winter stress on the beaches due to high wave energies and cold eliminate much of the biota, but just seaward in the surf zone and exposed at low tides are surf clams on both coasts. Of all the systems receiving pollutions of surface floating wastes, the beaches are most affected although the capacity of a high energy beach for processing and mineralizing wastes is also large. Where wave energies are somewhat less, additional species such as sand dollars become important and latitudinal differentiation appears.

High Velocity Channels (A-3)

Especially in northern waters of Maine, Washington and southern Alaska where large tidal waves are absorbed in archipelagos and inlets with deep channels, some characteristic ecological patterns develop on the current scoured bottoms and in the highly turbulent plankton waters. Even though the salinities are high and waters much like the open sea in character, the absorption of the energy of the world tidal wave into 10 to 20 knots tidal currents provides a special energy source and a stress. The same system also occurs in a few places in lower latitudes where there are inlets and converging waters as at Aransas Pass inlet in Texas. The scoured bottoms develop reef-like growths of encrusting animals and plants. Estuarine plankton associations, not characteristic of the open sea, develop in the moving waters. With food transported in abundance to any organisms that can hold on, the density of attached life is large although not diverse. The large eddies in the channel waters support microscopic phytoplankton of large individual size. The eddies and effects of the earth's rotation produce gyrals and other means by which floating and swimming animals and plants can slide back and forth with the waters. Adaptative behavior also permits populations to develop within the zone, with reproduction balancing losses. The great turbulence permits little opportunity for phenomena of stagnant waters to develop. Aeration rates are high because of the rapid removal and stirring downward of surface waters. The high current velocity channels are often between ecological systems of much greater diversity seaward and landward. The stress at the zone of contact may produce low diversity. Whereas zones of contact of resting ecological system types on land sometimes augment variety of components, the reverse is the pattern in these high velocity channels.

Oscillating Temperature Channels (A-4)

The widely oscillating temperature system is well represented by the Cape Cod Canal connecting coldwaters of the Gulf of Maine to the warmer coastal waters of southern New England. With large tides on the north, tidal currents in the sea level canal surge back and forth shifting the temperature twenty to forty degrees daily, and providing enormous stress to organisms that normally are delicately tuned to provide optimum metabolic processing for effective work at the temperature of their customary existence. Although such widely shifting temperatures are not common, they hold great interest in our interpretation of the workings of estuaries. The canal provides an advance look at the kinds of phenomena that may become much more common with the operation of nuclear power plants. Their output of large volumes of hot water may eddy and oscillate into the estuaries somewhat in the manner of the Cape Cod Canal. Also, the channel has some similarities with the proposed sea level canal in Panama where cold upwelling waters of high tidal range in the bay of Panama to the south will be surging in a sea level canal and alternating with warm Caribbean waters of the type that support Coral reefs. As already mentioned in our preliminary discussion, stress reduces diversity, and in the Cape Cod example there is a very low diversity system, including the stress-resistant algae Ulva and some tunicates and bryozoa, much less than that in the marine waters at either end. Systematists have imagined great invasions of faunas spreading through such a channel, but this example suggests the mixing channel may be a barrier, although the stress of oscillating waters may develop stressed zones near the mouth in which faunas of the side with most stress may be most compatible.

Sedimentary Deltas (A-5)

When great rivers carrying heavy sediment loads reach the sea they deposit sediment so fast that a special environmental condition is created with some features of stress, and a characteristic ecosystem results. One special energy stress is the simple downhill fall of sediment. If the river has been in position for very long it may have filled its bay and built a fan of sediment out into the ocean as does the Mississippi, the Altamaha of Georgia, the Brazos of Texas, or the Yukon of Alaska. Accompanying the river flow are varying discharges so that the delta waters are frequently stressed with sharp oscillations of high and low salinity as well as by the stress of blanketing silts. Although organic matter usable as biological fuels are incoming in the river waters, substrates upon which to support filter type animals may be quickly covered. Heavy turbidities shade out sunlight capable of supporting phytoplankton, at least until the plume of water slows down, drops some sediment, and becomes a lens of low salinity water further out on the sea. The zone of heavy sedimentation is as much a property of the inflowing water as of its own indigenous processes. Much organic matter gets covered over too fast for consumption, and mineralization is not efficient by the community or organisms with little diversity and specialization. These systems are among those now receiving the most wastes, which if not readily absorbed or decomposed in the sedimentation may remain in the waters moving laterally to stress other systems. As one moves away from the zones of maximum stress other subsystems occur such as oligohaline water systems, oyster reefs, marshes, and clam beds. The main delta deposition itself is dominated by geological processes, colloidal actions on clay, and microbial action.

Hypersaline Lagoons (A-6)

Where sea water flows into shallow lagoons in climates with more evaporation than runoff, salinities rise and briny conditions develop. High salinities require special adaptations by organisms in control of permeability and kidney actions. Diversities diminish and highly characteristic systems develop with a few species of phytoplankton, zooplankton, clams and fish in waters above 50 parts per thousand. Above 100 parts per thousand, there is mainly a system associated with Brine Shrimp. In general evaporite climates occur mainly in the sub-tropics in the U. S. represented by south Florida keys and south Texas. Small areas are also found in tropical zones as on the lee of trade winds on islands such as Puerto Rico and Hawaii. Wherever the briny lagoon develops, its faunas are characteristic even in temperate zones where cold seasons interrupt processes. Natural briny conditions are often associated with high turbidities that are associated with poorly vegetated surrounding lands and flash flood run-offs. High organic levels also develop because of the generally poor efficiency of the simple system in processing organic food chains within the organisms. Briny lagoons have low oxygen storage capacity and being enclosed may be readily disturbed by wastes and other processes. A special domesticated version of the natural briny lagoon is the salina considered in this report as a man-dominated system.

Blue-Green Algal Mats (A-7)

Apparently occurring whenever marine waters are very shallow, a few inches in depth or less are the blue-green algal mats that form blue-green carpets of microscopic interwoven living threads over which winds wash waters that have 10 to 30° C diurnal temperature range, large salinity variations with rain and evaporation, and almost anaerobic conditions of oxygen content at night, contrasting with daytime supersaturation. Vast sheets develop in south Texas and in local areas in other states. The system has a few species of blue-green algae, water bugs, brine top minnows that can gulp air, and micro-organisms. The natural system makes food photosynthetically more easily than it consumes it and much organic matter is left in the sediments. The system occurs in small extent as the uppermost band in the splash zone of rocky sea fronts. The mat system is also characteristic of many kinds of man-dominated waste systems. This is an example of the principle stated in the introduction. Systems adapted to natural stresses are often preadapted for invading man-stressed systems.

B. Natural Tropical Ecosystems

The characteristically tropical ecosystems are those with low energy stress of salinity, temperature, or other factors so that much energy of special adaptation goes into diversity and organizational behavior. These systems have many species, much chemical diversity in the many species, animals that perform complex programs in their life histories and service to the system, and bright colors associated with these programs. Low temperatures and sharp seasonal programs are not required although specialists have species life cycles on seasonal schedules. We consider these in order of the proximity to shore. The tropical systems have members which serve actively in cutting back the development of alternative systems. Thus fishes of reef habitats tend to graze back meadows that might otherwise be prominent.

Mangroves (B-1)

Mangroves are marine-based forests which have special adaptations for roots in salt water, and in anaerobic muds. Some species cleanly separate freshwater from salt, after which the freshwater is transpired through their leaves as part of the drive for the system. Complex branching roots support a great diversity of marine animals and the crowns carry many terrestrial animals. In some parts of the world near great rivers or near great tidal shifts as in southern Panama the mangroves receive much salinity stress and their associations are not so diversified. In parts of southern Florida, in Puerto Rico, and in zones of Hawaii where mangroves were only recently introduced, tides and river shocks are less. The upstream damming of the "rivers of grass" of the everglades has increased the role of the mangroves in the thousand islands of the lower Southwest coast where once freshwater discharges were larger and more erratic. Mangroves find their northward boundary with killing frost in Florida and Texas. The mangrove system controls sedimentation, and is a hurricane protection to some coasts. Mangrove systems return to the water organic nutrients of special character producing special plankton associations, including luminescent and brown waters. Mangrove forests are used for forestry purposes but may have higher value in coastal protection and buffer purposes. Mangroves are receiving wastes in Puerto Rico.

Tropical Inshore Plankton (B-4)

Because most plankton studies have been made in transient conditions in laboratories or in the strongly pulsing seasons of the temperate and Arctic regions, and because the high metabolic rates per gram and small storages in plankton give them rapid turnover times, plankton systems are often regarded as inherently unstable. In many tropical bays on dry coasts where they are not shocked with varying runoff conditions, enclosed bays develop highly diversified, indigenous, and very stable plankton populations.

The phosphorescent bay of Puerto Rico is a famous example where the steady light of a dinoflagellate phytoplankton species and its associated zooplankton have been continuously examined for many years, with only an occasional interruption as with high tides of passing hurricanes. There are special nutrient requirements of specialized tropical phytoplankton which explains some of the means for diversification. Thus organic nutrients are important in such phenomena as red tides, in inputs from mangrove swamps, and the movements of larger fishes. The shapes of bays and tidal exchange rates are important to maintaining correct nutrient media. Of all the tropical systems these may be most sensitive to disturbance by turbidities enrichments, or modification of navigation channels.

Coral Reefs (B-2)

Long heralded as the most diverse, most highly organized, and aesthetically the most pleasing of all ecosystems, the coral reefs occur in waters of bright sunlight, and uniform salinity and temperature, and moderate wave energy and current. A coral reef is made up of animals that form skeletons of self-made limestone and that incorporate microscopic photosynthetic plant cells borne on and within the tissues of the animals and rock structures in intricate symbiosis. Coral reefs are best developed in the U. S. areas in trust territories of Pacific islands, but small and beautifully diverse examples occur in Puerto Rico. Somewhat less developed reefs are found in the cooler waters of Hawaii and on the Gulf stream margin of the Florida keys where an underwater National Park provides protection.

As reasoned in our introduction, the lack of stress leaves much energy for a variety of combinations and diversifications. One result of having more variety of species with special adaptations is more variety of systems. Within the general category of coral reef there is greater variety than in other systems categories where possible permutations are less.

Because coral reefs are dependant on moving waters and on bright light, they are very succeptible to destruction by turbidity shading either from dredging or from microbial turbidity that may accompany nutrient fertilization. Although general features of coral reefs are readily described because of the great variety, there is less order and predictability available about the details of coral reef management. There is a large literature on classification of coral reefs, most of it based on areas outside of the United States.

The limestone substrates serve as a kind of soil and most of the animals have some means of eating limestone substrate for regenerative purposes. These adaptations hold the reef strong in relation to current and wave and may be essential to the prevalence of the coral reef over some more inshore types.

Tropical Meadows (B-3)

In tropical coastal waters where there are soft sediments and usually in slightly deeper water than are the coral reefs, one finds the underwater meadows of turtle grass and other plants. The broad expanses of green meadows of vascular plants and benthic algae support a very high rate of production that is aided by the currents that accompany this ecological system. There are many bottom animals in these grasses including filter feeders that work towards maintaining plankton too dilute to be a shading competitor. In full tropical form the tropical turtlegrass beds resemble the temperate eelgrass but are much more diverse, have little of the sharp seasonal cycling, and often develop white sediments because of the predominance of calcium carbonate precipitating animals like sea cucumber and urchins maintained in the grass system. At its more northern zones in Texas the turtle grass beds resemble the eel grass more.

Blue Water Coasts (B-5)

The deep blue waters of tropical seas have a characteristic pattern of deep light penetration, sparse plankton-based food chains associated with a generally low nutrient availability, and some fast recycling of nutrients by tiny cells and many diverse specialists among the animals. Blue tropical waters of this type bathe the Hawaiian Islands, Puerto Rico and the southeast coast of Florida in the Gulf Stream. The blue water system has the stress of vertical mixing and low nutrient problems but has little stress in temperature and salinity or other ranges. Such waters become the province of this summary of coastal systems where lands drop off steeply into the sea and blue water flows along the shore. Except for the special condition of low concentrations of nutrients, the blue waters have less stress than most plankton waters. With deep mixing, there are adaptive problems of maintaining plankton within the light zones. Although sparse in mass, the small plankton are in vast diversity with many shifting combinations possibly forming delicate adaptations to slight differences in conditions of these tropical waters. The low nutrient character makes these systems very sensitive to change by wastes. Fairly clear green waters from the open seas bathe other portions of the United States at other latitudes, but the plankton populations there are seasonally programmed, and different in character.

Natural Temperate Ecosystems

Between the latitude in Alaska where winter ice phenomena are important and the latitude of southernmost Florida, south of which seasonal changes in light and temperature become less important, are the natural temperate ecological systems which include the best studied estuaries and shores of the east and west coasts of the United States. Natural temperate systems are characterized by a sharp seasonal pulse in both light energy and temperature, requiring adaptations for control of metabolic rates. The range of the pulse is greater as one goes northward to Maine and Southern Alaska. Characteristic of such estuaries are the blooms of plant activity in the spring with maximum photosynthetic production in the summer. A food source is the considerable organic matter which runs into the estuaries from the rivers, and this flow also has a maximum on both east and west coast of the United States in spring and early summer because of the seasonal excess of rainfall over evaporation reaching its maximum then. Thus for two reasons the pulse of food available to estuarine ecological systems usually has a surge upward in spring and early summer.

There are many subsystems of interest and importance such as intertidal zones, shallow plant bottoms, oyster reefs and clam-worm flats, that live off import of food in passing water and estuaries that are plankton dominated. The basis for each temperate system of our classification is discussed next.

Tidepools (C-1)

Where the spray of breaking waves and high tides elevate water up into irregular, rocky sea fronts, water circulation is maintained in perched tide pools in which small and often beautiful communities develop that have great asthetic value in the coastal economies related to recreation and the education of school children. The high and little varying salinities of the cool waters flushing these pools provide a steady medium especially in those areas with much coastal cloudiness as in the Pacific Northwest and in Maine. In more southern locations with less tidal range, less wave spray and higher temperatures, daily heating provides more stress especially of wide daily temperature ranges. Where stress is not large, however, the large, colorful, and delicate starfishes, anemones, worms, and other animals form complex animal cities. These coastal systems develop slowly, are readily destroyed by pollutions or excessive collecting. They serve as coastal indicators of the quality of the waters bathing the shores. The tide pool systems are restricted to the thin line of surf where rocky substrates are suitable. In the grand perspective of America's resources, the tide pools have values as wilderness zones for national park-type usage. Their complexity provides to the continental United States the type of diverse systems one associates with the stable tropical regimes in which basic studies of organization and behavior are possible. Theorists are now relating these kinds of studies to the general problems of behavior, structure, and maintenance of the urban cities. Some tide-pool tracts are thus needed in the research programs that ultimately concern the principles of stabilization of our society for which suggestions as to special mechanisms are drawn from ancient examples of the sea margin.

Bird and Mammal Islands (C-2)

In some areas where there are large ranges in the pulse of the sea's coastal productivity there are colonies of birds and marine mammals that concentrate in dense rookeries on isolated islands or rocks there providing for safety of young. The animals during their summer occupy a subsystem with some of the same role in the coastal systems as migrating fish, accelerating food gathering in summer, drawing large energies from the sea at the time excess energies develop. As the productivity system declines in autumn, the young birds grow up and fly away, distributing their energy demands southward. The bird island with its foraging operations many miles in all directions is part of the regulation system of the coastal system. The large flying birds serve as nutrient concentrators, and locally the rookery locations have extreme concentrations of nutrient fertilizer which may go back into plant growth systems either of nature or man. The quantitative magnitudes of these cycles are only now being calculated relative to their supporting system. The bird islands may not only be of aesthetic values in human coastal recreation but important and as yet, little understood in service as a control agent to prevent localized over-concentrations of smaller crustacea and fish populations. In the migration of birds and mammals equatorward in winter and back northward in summer there are the means by which there is coordination of the whole biological economy of the hemisphere. The problem of preservation and maintenance of this system of stabilization for wide areas of the coastal and offshore seas usually involves special consideration of the summer rookery sites. The ability of these consumers to switch to whatever is in excess makes this role possible. The question of pesticide concentration in this system is now under scrutiny.

Landlocked Sea Waters (C-3)

Mainly outside the scope of a coastal classification are the landlocked sea waters which can receive marine organisms physiologically, but being separated from population pressures, from the estuarine to open sea migrations, seasonal nursery pulse, and tide tend to develop ecosystems with some freshwater affinities and many organisms from salty lakes. These waters are mentioned as a source of information on the consequences of cutting off estuaries from the sea.

Oyster Reefs (C-5)

Wherever there are strong current systems bringing suspended material that may serve as food, filter feeding animals may concentrate into dense, exposed cities protected by hard masses of their skeletons. The reefs built by various species of oysters are the most common types, but reefs of animal consumers also include great sheets of mussels, serpulid worms and other animals. Oyster reefs are consumers requiring organic food in particulate form. The conditions for consumer reefs are very different from coral reefs that are mainly based on their use of light in photosynthetic food production within their tissues. Oyster reefs develop in the intake pipes of industrial plants that use salt water for cooling, on bars where waters circulate in estuaries, on the sides of rocks, on pilings, or on bottoms of ships. Because of their concentration of life and structure the reefs have been of great importance as food for man, and the shells have become important in calcium carbonate industries such as road building and concrete manufacture. The management of oyster reefs has not always been made with the understanding that the reef is based on the continuous circulation of a much larger area of water than that over the reef itself. The planktonic farm and the organic matter from rivers that contribute support to the reef are large in volume. The foods dispersed in a bay are controlling the amounts of reefs. One cannot manage a bay for oysters without managing the inputs of suspended foods and the release by oysters of minerals that return to the plankton as a necessary step for growing more food for the oysters.

Because oysters are built with shells, have wide salinity tolerance, and abilities to suspend operations for long periods, they are adapted to great variations in water level, salinity and temperature in the river mouth estuaries or in the intertidal zones. Where stresses are less, more diverse communities replace the oysters, doing so by spread of drilling snails and action of diseases that eliminate the oysters, as the conditions become stable enough for the competing communities. Although the diseases and carnivores are often the agents of replacement of oysters by more diverse ecosystems in the course of a season or in year to year changes, the ultimate causes are related to the changes in regime that allow more stable, higher salinites and more uniform temperature conditions that foster the complex systems.

The management of oyster reefs has to be related to the programming of river control, towards maintaining oscillations, and insuring adequate volumes of suspended food particles. Leasing bottoms may not be enough to provide good management, unless the whole bay system is leased and managed as it is now done in a few states.

Salt water mussels form enormous reefs especially in northern latitudes where they hang on the rocky substrates. Since they form rigid structural mats of animals, they too are consumer reefs. Among the most interesting of ancient geological records are those left by ancient consumer reefs that begin now to yield their information about ancient estuaries as we learn how to interpret the whole estuarine systems interactions from the nature of the fossil reef subsystem.

Marshes (C-4)

Where there are broad intertidal flats of soft sediment not too strongly stressed with waves and winter cold, grassy marshes develop in the estuarine salt waters that flood the grass usually twice a day leaving the systems standing free in air part of the day. With green vegetation out of the water, but with roots in wet rich sediment, marshes are among the most productive of organic matter of all systems. The alternating tidal exposure does have some aspects of stress requiring special adaptations. Marsh grass and the animal populations of oysters, snails, and fiddler crabs are capable of maintaining both submerged and emergent existence.

Many special adaptations exist in the marsh. For example, some tiny microscopic diatoms burrow into the mud when the tide is in and then surface on the mud during outgoing tide there receiving light for their photosynthesis. The phenomenon turns black mud a golden brown within minutes as the cells emerge.

The marshes have been shown to export much plant matter to the estuarine waters where slow decomposition begins after which the soup of organic food supports much of the food chains. Consumption by clams, oysters, and shrimp remineralizes the fertilizer elements which are released to the marsh grass completing the cycle. Recognized now by a court decision in Massachusetts, the marsh is an inherent and necessary part of many estuarine ecosystems. Removal of the marsh would be tantamount to removing the most productive part of the farms from a system of farms and cities. Marshes increase in importance southward in the United States because the coastlines of intermediate tide and wave energy and other factors of geological history develop broad sedimentary platforms. Winter stress on intertidal zones is also less and although the tops die back in winter, the root systems are available for a fast spring growth. With their productive structures above the water, these systems may have more capability for survival under some waste stresses and thus may have more capacity to serve as self-purification than some other systems that are dependant on clear water or are not already adapted to some stress. The patterns of two main types of grass Spartina and Juncus are almost universal on the east coast. A Salicornia predominance exists in many west coast marshes, most of which are relatively small in extent. In the ice stressed estuaries of Alaska some other types develop.

Worm and Clam Flats (C-6)

Animals that provide for their security by burrowing in flat areas of sand and mud may predominate the area and develop characteristic subsystems based mainly on the particles of food that pass by and are then filtered. These flats may be intertidal or permanently submerged. Like the oyster reefs they are usually dependent on the food in water of a much larger support area that passes over the flat and is then filtered by the clams and worms. In our classification, we may find Mya and other clams in two places; one as a clam flat subsystem when considered alone, or as one component of the deeper estuarine systems in which the bottom is a contributor but not dominant. Some microscopic plant contribution to food may come from the flats themselves when they are close to the surface receiving considerable sunlight, but they are too stressed for benthic plants of larger size. The commercial Nereid worm flats in Maine may be of this type.

Clams with long input-output siphons such as Mya arenaria are especially adapted to the intertidal zones which have temporary surface stress. Thus the Mya predominate in northern flats that have strong freezing winter winds between tides. Deep siphoned clams are also found in very shallow mudflats of Texas, where the surface muds become very hot for a few hours, but the deeper muds remain cool. Long siphon surf clams, Spisula, are part of the subtidal beach zone system where the long siphons allow the clam to live below the zone of greatest sand disturbance and thus to avoid being unearthed and broken. Mya with ability to take salinity stress also is characteristic of the oligohaline zones.

In southern regions the oligohaline zone is partly dominated by Rangia which lies on top of the mud in enormous numbers, its protection from an extremely heavy calcium carbonate shell instead of from a thin shell and a long siphon. These two species occur in enormous numbers and are a major resource. Adaptations to respire without water pumping are part of the special requirements of the intertidal flats. The big worms carry haemoglobin and the clams have means for use of oxygen in air.

In the extremely stressed intertidal zones of the north or of the upper estuaries low diversity populations are almost entirely of one or two species. In the more stable high salinities of coastal waters further from river surges, the diversity overall is large but there may be local beds of one species, a specialization phenomenon discussed in the introduction.

Because the filter feeding clams are related to the nature of the passing planktonic food or detritus and also have adaptations that reflect special stresses, they may be used as indices to classify estuaries of which the clam beds may be only a subsystem.

Eelgrass and Benthic Algal Bottoms, Shallow Salt Ponds (C-7)

In shallow waters with good current, where salinities are high and little stressed with river surges or light-absorbing turbidities, a bottom system of dense bottom vegetation develops with blades of grassy eelgrass or bottom algae of massive type. The heavy beds of underwater vegetation wave and weave in water currents providing some of the highest known photosynthetic food production situations in the sea. The currents assure necessary nutrient inflow and waste removal from the blades. The association of animals and micro-organisms is complex and varied as one expects when energy input budgets are high and when stresses are small. Eelgrass beds are found the world around, being important on both coasts and Alaska. Differences exist with some substitutions of fauna in niche roles. In Alaska, for example, herring deposit eggs on the eelgrass, and their larvae may shelter in the eelgrass beds, whereas the safety of herring reproduction on the east coast is insured with schooling behavior and the return flows of larvae of coastal gyrals.

On the east coast there was a widespread demise of eelgrass beds in which a fungus disease was implicated thirty years ago, but in the last 15 years it has been coming back and is often again a major system or subsystem. The disappearance did not take place on the west coast even though the disease organisms have been shown to be present in the beds. Many scientists believe the disease agent was not the primary cause of stress that allowed the eelgrass to be replaced, although it may have been the agent which went into epidemic state when the conditions for effective eelgrass were stressed. One possibility is the increase of turbidity of estuaries associated with the cutting of eastern forest, poor agricultural practice and soil erosion, which may have reached its peak at the time of the economic depression, the time of the eelgrass die back.

As pointed out by Nelson Marshall most eelgrass is accompanied by some clams or filter feeders (such as bay scallops) that may have an important role in clearing the turbidities from the waters so that high production of the grass can support a large microbial population decomposing the grass and in turn supporting a high density of filter feeders. Heavy benthic grass beds in upper estuaries have freshwater plants like Valisneria, and in the Gulf regions the eelgrass beds are replaced with more tropical plant dominants like Thalassia although the general characteristics of the complex association of animals in the beds are more those of the eelgrass than that of the tropical grassy meadows. This may be related to the sharp seasonal program that exists in the productivity system in the Gulf requiring animals with strong seasonal programming.

The benthic plant systems occur in isolated shallow bars in deeper turbid bays, as continuous communities in channels, and as the main pattern in salt ponds (as in southern New England) in which the inflow and outflow of tidal waters organize the patterns around the fan of spreading tidal distributaries.

Oligohaline Systems (C-8)

Studies the world over have shown that the minimum diversity of species is found in river estuaries in the zones where the salt ranges from freshwater to a few parts per thousand. It is not this particular salinity that is the species restricting stress, for there are special estuaries of this salinity in Florida and elsewhere in which the waters are spring fed and very steady. In these estuaries great diversity does develop with complex mixtures of animals one might otherwise regard as marine and animals one regards as freshwater types. In the usual estuary the 0.5 to 8 parts per thousand range is the zone where there is the most fluctuation of irregular surges of river water during high rains followed by surges of salt water back during exceptional tides and low river discharge. In northern latitudes there is the additional stress of very different land runoff temperature contrasting with less variable marine waters. The oligohaline regimes thus are fluctuating regimes with only a few species of plants and animals. Clam bed and subsystems are usually important. The deep digging Mya clam dominates in the north and the heavy shelled Rangia dominates the oligohaline zones to the south. In a state like Louisiana with predominant phenomena of the large river discharge of the Mississippi the oligohaline regime is the main estuarine phenomenon and Rangia clams are the main animals inshore from the better known oyster reefs, the latter marking the seaward margin of the oligohaline zone as we define it. The oligohaline regime has some freshwater and some marine fishes participating especially during temporary period of salinity stability.

Medium Salinity Plankton Estuary (C-9) Also Mixed Salinity Plankton Estuary

The image most people see when one says "estuary" is the medium salinity, moderate depth bay, which has much fishing but not much visible evidence of anything else. The bays draw support from food chains of invisible microscopic plankton supporting the characteristic populations of crabs, fish, and commercial shrimp. Many of our largest estuaries are predominantly of this type although they are often fringed and bordered by smaller subsystems of other types. High nutrient levels and good stirring mechanisms generally produce high photosynthetic rates wherever clarity of water is maintained although it is less than in systems like the marshes that have less water to absorb light.

In winter, with low light, and well stirred waters due to tidal shifting and some turbidity from rivers, the plant cells spend too much time in the shade and stop making much food. In the spring as light conditions increase, the critical condition at which the plant cells can make a net gain is reached and there is a sudden bloom of some of the diatoms that sets off the seasonal production sequence. During the winter there is organic particulate food remaining from the previous season, from marshes, from rivers, and other storages that keep some of the animal life going. With the rising burst of plankton growth there are some releases of larvae from clams, oysters and barnacles, and little water-flea-sized copepods develop. Acartia predominates this system throughout the east coast. Middle salinity examples documented on the West coast with Acartia copepods include the Yaquina (Frolander, 1964), the Sacramento -San Joaquin Estuary (Kelley, 1966), and others. Reproductions and migrations of shrimp and fishes that eat the zooplankton are timed to coincide with the increased yields of these small components so that the rise in stocks and consumption takes the rising production, most of which is entirely invisible to the man in the boat above unless he measures the phytoplankton, some index of its activity such as oxygen production, pulls a zooplankton net, or has some way to estimate the rising stocks of fishes and shrimp. The middle salinity estuary has species with some ability in their kidney systems to deal with salinity fluctuation, some ability to switch food intake from organic matter to plant plankton base, and an effective temporal program for migration and reproduction so as to hook the need for more food to the timing of appearance of more food.

Whereas the bottom clams and the special subsystems of the bay margins are contributors, the main system is one of plankton and plankton eaters. As the sunlight begins to decline after July, the population growth and reproduction declines and soon many populations migrate out again decreasing their load.

Because the source of energy of this system is in microscopic plant plankton, from invisible organic contributions from the rivers that support bacteria as intermediates, and from energetic services of tidal currents, rarely do persons not trained in marine science understand the basis for this system and its management. The food chain is out of sight and thus out of mind. The need for maintaining effective plankton populations is not understood by the untrained resource manager. Since all the species draw from some of the same energy pools, rises in or falls in one species must be accompanied by compensating changes in others. This system like the others must be managed as a whole, not species by species or with commercial fish separate from sports considerations, etc.

The medium salinity estuaries often have partial stratification with wedges of dense salt water underneath. In systems allocated to this type, mixing is adequate to prevent anerobic conditions from developing at the bottom even though oxygen is less there since respiration is more at the bottom of the estuary than in the top water. Estuaries tend to be deeper as one goes north, but **also** the amount of tidal energy available for currents and mixing **and eddy diffusion coefficients increase.**

Sheltered and Stratified Estuary (C-10)

Most of the estuarine systems have strong tidal or wind-wave circulation that serve the communities by doing necessary work of circulating materials: moving the needed carbon dioxide and nutrients to the plants, needed food particles to the animals, needed surface oxygen to all concentrated sources of consumption and decomposition down below, larvae from sources of reproduction to sources of larval feeding, animal populations from summer situations to winter locations, etc. Stirring systems thus are used by adapted species as auxiliary energy sources to do jobs they would have to do for themselves. In the absence of the circulation they either survive in reduced numbers or are replaced by slower operating species which can operate in the less energetic situation by requiring less. The stirring currents can also be a source of stress when they move populations from places of support to places where they are not adapted. Experimental studies show that there are optimum rates of circulation and that too much energy leads to loss of diversity and ability to develop as much production of living work.

Due to geological events in the formation of the estuarine margins, some **bays** are sheltered from winds by being small or thin and crooked in shape, so that winds cannot build up much wave action. If the bays also have a shallow or narrow mouth large tidal flows cannot exchange much water into the bays and relatively stagnant estuaries develop, which may **exhibit** the vertical stratification one associates with a fertile lake, a system with an upper oxygenated layer and a low oxygen subsystem below, dominated by a microbiological decomposition pool for at least part of the year. There are not many of these systems but the ones that exist are of considerable importance in indicating what is possible when these kinds of estuarine embayments are constructed. Many of man's actions in changing circulations inadvertently, in dredging channels, in diking estuaries for power or water storage, and for other purposes are making new systems of this type. Stratified systems are much more sensitive to pollution effects than the better mixed ones. A fjord is a narrow deep channel cut by a glacier originally and now invaded by the sea. Fjords are one of the kinds of basins which may have restricted circulation and stratified estuarine type of phenomena. Some of the best data come from Canada and Norway.

Kelp Beds (C-11)

At depths less than 100 feet seaward of the surfzone or in high salinity embayments where there is some swell and clear water, giant brown algae grow as vertical-standing, underwater forests that wave and lash with the sea motion, supporting a productive plant production at the top and a very complex and organized ecological system. Kelp systems have maximum development in cool waters of the west coast with Macrocystis. In the Atlantic Laminaria fills the kelp zone. Chapman (1964) summarizes studies by F. T. Walker giving weights and cover of these beds. This study is possibly pertinent to appraising the system in Maine. The kelp is cut and harvested commercially on the west coast. In Maine the associated red alga Chondrus cris pus is harvested commercially. The controversy developing about the effect of pollution or urchins on kelp has led to many scientific studies and some experimental attempts to protect the beds by dropping flaked quicklime on urchins. Ecological considerations at the ecosystem level may not have been adequately considered so far in this work. An inherent feature of the undisturbed kelp system are large specialized fishes that are supported on well channeled food pathways from the kelp, but which have the tendency to eat and remove those members that are dangerous if too abundant in the kelp system such as urchins. On the other hand urchins form a system with encrusting algae and while supported by encrusting algae have a tendency to eliminate the kelp system by eating the bases so that the kelp stands float away. In effect each productive system has special members it supports which exert negative and competitive actions on the other system in such a way as to favor its own system. If pollution stresses the special fish consumers of the kelp bed so as to eliminate their action, then the urchin systems may displace it even though the waste action on the kelp plants is neutral or stimulatory. As in so many other situations, stresses that work against the control systems displace the large and complex system types in favor of the simpler systems that rely on rapid replacement instead of organization.

The kelp beds have importance in their own beauty, as a system of potentially greater harvest, in their contribution to coastal productivity, and in their value to the understanding of competition of whole systems through interaction of their top food chain animals on adjacent systems.

Neutral Embayment and Shorewaters (C-12)

Washing the outer **archipelagos of** Maine and Alaska, into the zones at the mouths of some of the largest estuaries, and along zones of Florida where there is little freshwater discharge are plankton waters of the Neutral System.

In the Pritchard salinity classification, an estuary without river inflow or without an excess of evaporation was said to be neutral, one in which a bay is filled with water exchanging with the open sea without salinity change. Neutral embayments and coastlines with steep fall-off have waters that move in from the sea without much modification except that the waters **have no longer the deep** scattering layer migration and have a bottom below. Also at the coast waters receive a different kind of vertical stirring as tidal wave energies are absorbed among islands in channels or reflect off shores. The neutral system is a high salinity plankton system that has more diversity than most estuarine systems, but is dominated by recognizably different species. With clearer waters than most estuaries, the photosynthetic zone is deeper, and variations in salinity and temperature **are less.**

The neutral waters are close enough to be affected markedly by land influences such as waste outfalls should they develop. The neutral system in such instance is readily transformed into a new type.

With more stability of temperature and salinity due to the depth and sources from the open sea, **neutral shorewaters** probably have the highest diversities and complexity of components of coastal plankton systems of the temperate latitudes.

Whereas high diversities tend to favor little mass and yield of any one component, the phenomenon of local species cities and the movement of the high pulse stocks of shrimp and migrating fishes of the estuaries back into the high salinity zones, make commercial concentrations available there too. The coupling of a stable salinity system to a pulsing one leads to pulses in both.

The coastal neutral waters are also the zone of migration of coastal fish migrations northward in the spring and early summer and back in the fall, supported in the southward migration by the populations emerging from the bays. The neutral system is thus a giant switching system of the network of food distribution and processing of the planetary migration with estuarine system in which man's small trawlers participate.

Natural Arctic Ecosystems

The coastal systems of the far northern latitudes receive heavy stresses over much of the year from ice phenomena and receive photosynthetic energies for only a short period in summer. With more light and photosynthesis on land but more winter stress, much of the production of the land is not processed there on the land but washes into the sea before processing. Ecological systems develop in, on, and under ice and in the fjords associated with the glaciers. Those systems of Alaska with ice phenomena predominating their regimes are grouped as Arctic. The other systems of southern Alaska are variations on temperate systems also found further south. Those Alaskan fiords without glaciers or glacier fed rivers were classified with other neutral embayments.

Glacial Fjords (D-1)

Many of the glaciers of southern Alaska terminate in the estuaries where they carve small and large blocks of ice and directly discharge much matter enclosed in and on the glacier. Waters are blue. Some features of this situation apparently lead to large populations of marine animals at the base of the glacier. Meltwater tends to form a freshwater lens over the top of the estuarine system, but the saltier waters below do not ordinarily develop low oxygen because of the high tidal exchange that takes place below the surface lens.

Turbid Outwash Fjords (D-2)

A different type of ecological system develops in fjords that receive turbid rivers from glacial deposits where the glaciers end on land. Heavy sediment loads affect the densities of the inflowing meltwaters, which are heavy enough to mix downward into the estuarine system producing a different pattern of circulation and exchange.

Ice Stressed Intertidal Zone (D-3)

In the Arctic and subArctic the intertidal zone is stressed by freezing between tides where waters are ice free and by the thrust of sea ice. The high energies of winter waves and tide from the Aleutian center of cyclonic low pressure pound the intertidal zone in winter on high tide, and strong subfreezing winds stress the zone between tides making impossible much intertidal life through the winter. Summer conditions permit development of algae and small sized populations. On the north side of Alaska the sea ice scours the coastline.

Sea Ice (D-4)

Sea ice harbors life. The freezing and melting of ice and snow develops nutrient concentrations in and on which algal blooms develop. Large mammals may also make contribution. Algal associations are on the underside of floating ice with interesting photosynthetic production in low light intensities, The ice provides a form of stability to its underside, including nearly constant temperature and protections from wave action, wind stress, etc.

Under Ice Plankton System (D-5)

In Arctic seas on the north and west side of Alaska covered for the most part with sea ice, light is low in intensity and short in season, but plankton populations do develop regular patterns and good chains. At low temperatures organisms have less thermal stress so that structure is easier to maintain and under the ice there are fewer disruptions from waves and changing regimes of wind and temperature. Characteristic of these systems are the large mammals among the ice floes. The cover of ice provides special temptation for the disposal of wastes, discharging under the ice--something like sweeping dust under the rug. With the further development of Arctic industries such as those related to new petroleum discoveries, more will have to be learned about the ice-topped shallow plankton seas.

Emerging New Systems Associated with Man

At this stage in classification and study of emerging new complexes of pattern associated with characteristic wastes and disturbances by man, we can include only those types that have been studied enough to identify the presence of something new in pattern. No doubt the number of emergent new waste types will grow with efforts to identify them as well as with the spread of industries.

Although the types of waste and disturbance, which are changing the estuaries of America are of many types, most of them appear together in multiple waste channels. There are relatively few types other than the multiple-waste estuary. Apparently decisions as to location of waste outfalls by towns and industries have been much influenced by the presence of other waste outlets. With passing patches of man's effluents the mixtures might seem to be of endless variety. However, the alternating shock of contrasting chemical solutions do develop some common properties of high stress and low diversity, even though different kinds are represented.

Sewage Waste (E-1)

The discharges of raw sewage and the rich effluents from primary or secondary treatments inject high levels of organic matter and enormous increases in the trace nutrients required for phytoplankton photosynthesis. The nutrient ratios of such elements as nitrogen and phosphorus in the wastes of a city have some basic properties which vary depending on the industries using the same effluent system. These wastes tend to support both producers and consumers of types different from the unmodified system. The small red annelid worms at the end of ocean outfalls of sewage are one characteristic pattern. Although more attention has been paid to the survival of disease organisms in affected estuaries than to the nature of the emergent new system, the growth of cities will tend to convert more and more estuaries to a type of system compatible with these flows. Case histories already studied produce bases for characterizing these emergent systems.

Seafood Wastes (E-2)

Wherever fish and shrimp are landed and processed for food there may be wastes from the processing which enrich local waters and produce blooms and varying oxygen conditions. Since the wastes represent components from the sea, the return and decomposition represent the same kind of processes that would have occurred without the food harvests except that these releases are much more concentrated than the natural patterns and regenerative cycles much more irregular in discharge.

Pesticides (E-3)

The wide distribution of pesticides is well documented, but the kinds of ecosystems one gets when the levels are relatively high is only now being learned although some extrapolations of laboratory data can be made to predict the system. Most of the case histories available show disturbance of a system, but not as yet are there cases where the effect so dominates the system as to change its main characteristics.

Dredging Spoil (E-4)

Dredging changes depths and releases large volumes of sediments and turbidity. A number of case histories can be cited on the nature of artificial dredging effects, many of which resemble the natural patterns in river mouths.

Impoundment (E-5)

Estuarine system types change when circulation is reduced or when access of the sea is eliminated for purposes of converting estuaries into freshwater lakes. The reduction of wave and current energies eliminate estuaries of known valuable type. Recognition of the changed system may help in appraisal of the nature of the new type. There are closed systems with water composition like that of sea water which accept marine faunas and develop useful ecological systems after seeding and introductions. The Salton sea is one case often cited where new designs are developing new systems in waters cut off from the sea. Not the least of the changes is the elimination of migration.

Thermal Pollution (E-6)

The advent of nuclear power draws much attention to the systems which develop where sea waters are drawn into cooling pipes and returned to bays. Whereas the patterns of low species diversity and physiological adaptation are well established in studies of natural hot springs, the patterns in the cooling water are complicated by variation in rates, by variations and interactions with adjoining systems of older types. Thus the several situations already in existence are studied carefully for some indication of the type of ecological systems that may prevail. Two natural situations of temperature variation are the hot salty ground waters discharged from oil wells and the fluctuations in temperature, lowering diversity, in the Cape Cod Canal in Massachusetts.

Pulpmill Waste Systems (E-7)

In quantity and volume the wastes of preparing wood for paper are vast on all coasts with many estuaries dominated by release of organic materials fiber, and chemical waste from processing. There are the organic substances diffusing from wood rafts in Washington State, the river bottoms of Maine with sawdust sediment, the lignin by-products from the paper processing, and the sulfites and other chemicals which have toxic aspects. The separate laboratory test of components have long been studied, but the overall behavior of an estuary dominated by this influence is not easily documented. It is not clear, for example, if the microbial food chains based on the organic matter lead to higher food chain productivities or not. The freshwater zones of such rivers sometimes are dominated by growth based on soluble organics such as Sphaerotilus, which forms fungus-like bacterial colonies that densely drape all surfaces. What really happens with this slime in the estuaries is less clear.

Sugar Cane Wastes (E-8)

With sugar cane the soluble organics are not released, but the fiber, wash waters, and much mud entrapped in sugar harvesting methods are sometimes flushed into clear waters of tropical coasts where turbidities are incompatible and disturbed systems result. Whereas turbidity injections from freshwater plumes are a regular pattern in moist tropical coasts, the waste into stable complex systems provides a different permutation.

Phosphate Wastes (E-9)

The mining of calcium phosphates from sedimentary deposits involves much processing of overburden soils. Waste waters have slimes with considerable fluoride, phosphatic content, and turbidity. If there is refining there may be other wastes which are acid with very high dissolved phosphorus and fluoride concentrations. The systems developing where phosphate wastes are released may have changed nutrient ratios relative to phosphorus and shading of turbidity. Estuaries associated with Peace and Alafia rivers in Florida and in the Pamlico area in North Carolina provide examples.

Acid Waters (E-10)

In freshwaters of states like Pennsylvania, a characteristic pattern of acid waters results when oxidation of sulfide deposits produces sulfuric acid. In our sea grant ponds at Morehead City, North Carolina, exposure of salt marsh muds to the air produced a similar acid condition in ponds with carbon dioxide driven off. Special phytoplankton developed which were adapted to fairly hard buffer systems and had little available carbon source, except free carbon-dioxide being released from animals. A characteristic plankton developed like that in fresh waters. Acid releases from industry or from mining are likely to generate this pattern, well known in freshwaters of Pennsylvania.

Petroleum Shores (E-11)

The frequent spills of petroleum have provided many examples of a special oil shore ecosystem, the best studied being the Torrey Canyon spill in England. Floating oil ends up on beaches and other shores where microbial processes carry out decomposition especially if other nutrients needed by the bacteria are present. Related to the petroleum is the pattern of toxicity and phosphorus fertilization from use of detergent to disperse oils. Oils are released from marine systems to the surface in slicks as a normal process, but the petroleum spill is vastly different in quantity. The action in stressing large animals, in forming toxic sludges on the bottom, and in permeating flesh of animals is well documented. Where spills are frequent, the pattern developing becomes a regular ecosystem of a new type.

Piling (E-12)

The introduction of wood piers and piling constitutes the creation of a special ecosystem type with shipworms and boring crustacea. Even with heavy creosote and other chemical treatments, characteristic boring animals such as gribble (Limnoria) do develop and apparently can consume the wood in this state. Setting of intertidal barnacles and other organisms on the outside tends to be fewer in number and type. Estuarine piling is a special system of man.

Salina (E-13)

The sequence of evaporation of sea water to form salt follows procedures that have been with man's culture for hundreds of years. Man's special arrangement of estuary flows for this purpose constitutes a special ecosystem. A steady state pattern of inflow and removal involves a rotation of treatments to a sequence of ponds. The arrangements for processing the water by man make distinct differences in the system as compared with natural briny lagoons that form otherwise in such climates.

Brine Pollution (E-14)

The flow of brine waters either from industry, from waste of extracting freshwater from sea water or from ground waters up through oil wells constitute a special condition. The brines have different ion ratios from sea water especially in having different cation ratios and often are laden with iron and other dissolved substances. Brine waters from inflows of this type differ in organic content from that developing in briny lagoons and salinas. Flowing brine water is dense and constitutes a stress where it fluctuates over normal bottoms.

Petrochemicals (E-15)

The refining of petroleum produces wastes of mixed organic compounds, and usually with refineries are located complexes of industries which use the various petroleum components in plastics and other manufacture, producing additional organic wastes, many of which are toxic. The mixtures of these wastes concentrated in small lagoons produce black waters, anerobic conditions, and very low diversities of biota generally. Less known is the pattern of ecological systems one gets when petrochemical wastes are dispersed into estuaries in more dilution.

Multiple Stress (E-16)

The most common disturbed system in urban America is the city harbor or upper river estuary which has ocean shipping, wastes from cities, industrial wastes of many types, dredging of bottoms, partial empoundments interrupting circulation and injections of thermal cooling waters. Diversity of species is small, larger animals are rarely in evidence, and chemical sensors and analyses show paths of contrasting waters drifting by, providing sharp shocks to all living organisms including the fouling communities on ship bottoms. Showing that a nearly dead ecosystem goes with multiple stress is no trick. The real question is to find some kind of adaptations that can function.

F. Migrating Subsystems

To the energy support cycle are coupled regimes of micro-organisms and animal activity rising with the energy availability. A characteristic adaptation to the seasonal regime that permits the rapid spring rise of animal populations is the release of microscopic larvae at the time of the phytoplankton blooms. Then there are migrations of populations of larger animals swimming or swept into the bays during summer from the rivers or from the open sea. Commercial shrimps, herring-like fishes, shad, and salmon make their famous migrations and may have the one common feature that the population's new young find their period of most rapid weight addition while in the estuaries, thus taking advantage of the pulse of food in that system. The general concept of the estuary as a "nursery" concerns the fast growth of newly hatched young rather than the actual reproduction. Egg production is often done in an area of safety as with salmon far up small streams where live eggs are stored in stream gravels over winter, or with shrimp and mullet spawning in stable temperature and salinities seaward in such a way that the young are drifted back into the estuaries. In other instances the eggs are released within the same estuary where the nursery function may develop. The important generalization about the estuarine migrants in the temperate systems is that a stock will continue to dominate the estuary as long as its programs of reproduction provide enough new young to take maximum advantage of the estuarine pulse of available food energies in the spring-summer season.

In one sense the migrating subsystems are the principal means for organizing all of the sea's systems into a coordinated whole.

Part II

FORAMINIFERA IN ESTUARINE CLASSIFICATION

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Among the various microconsumers of estuarine bottoms, foraminifera provide useful clues for the energy classification of estuaries. They not only participate in the cycling of organic materials but also accumulate energy in the form of protoplasm and a calcium carbonate shell or test. Because their tests are well-preserved after burial in sediments they have become a diagnostic tool, long used by oil geologists, for classifying ancient strata and recognizing oil-bearing deposits.

Foraminifera are especially useful for classifying estuaries because they live in nearly all systems from fresh water to the continental shelf and beyond. They form distinctive groups, possessing certain adaptive characteristics, in different types of estuaries. Therefore, each estuary has its own characteristic fauna by which it can be recognized. Furthermore, foraminifera are fairly abundant, easily collected, and readily identified. Because of their utility a wealth of knowledge has accumulated on their taxonomy, their distributions and ecology. As a result foraminifera are better known than any other widespread estuarine group. The purpose of this chapter is to show how they can be used to classify estuaries from which more refined information on estuaries can result.

LIFE AND ACTIVITIES OF FORAMINIFERA

Foraminifera are microscopic unicellular protozoa that develop a test composed of calcium carbonate, agglutinate sand particles (arenaceous) or occasionally, organic chitin. In estuarine areas they live on or near the sediment surface and often attach to benthic plants. Growth of the test leads to formation of chambers which are arranged in a multitude of different forms. Often, end chambers are contorted under stress conditions. Foraminifera gather food in protoplasmic nets extending around the tests, a feature which distinguishes them from other amoeboid protozoans. They trap a wide variety of algae flagellates or bacteria and cram them around their test or into an aperture through the test. Although pennate diatoms are among the most common food, different species have specific food requirements (Myers, 1943). Not only the type of food but the amount of food are of importance in foraminiferal nutrition (Bradshaw, 1955).

In experimental cultures Lee **et al. (1965) found that foraminifera are "bloom"** feeders. When low concentrations of food are present forams eat sparingly and reproduce slowly, but when food is abundant as in a bloom, they exploit it. These results are supported by a few observations in estuaries - for example M. Buzas (1969) found a periodicity in species density in the

Choptank River, Maryland, with relatively high numbers during periods of high chlorophyll content. Myers (1942) found foraminiferal growth increased during a phytoplankton bloom and furthermore the chambers added were longer, and thinner than when food was scarce. Similarly, Waldron (1963) found a spring "peak" of foraminifera in Timbalier Bay, Louisiana, presumably related to the amount of land-derived organic nutrients (Fig. 1). Although such temporal studies are few, they do indicate that foraminifera may be sensitive to timing of energy sources as freshwater inflow.

The life span of foraminifera ranges from a few months to several years. E. Myers (1943) found that the life cycle of the cosmopolitan species Elphidium crispum in tide pools of temporate regions is completed in two years, whereas below tide level 3 to 4 years are required. In tropical water by contrast the span is six months and a life cycle is completed in one year. In the life cycle there is a succession of sexual and asexual generations. Reproduction terminates the life of both sexual and asexual individuals and this feature provides a means of determining the annual productivity. The work of Myers (1943) and Glaessner (1967) are the chief sources of information on the life history, habits and activities of foraminifera.

FAUNAL FEATURES

To identify different estuarine types it is useful to organize distributional data under the following faunal features:

1. Number of specimens or abundance.
2. Number of species and diversity.
3. Shell characteristics and composition.
4. Number of planktonic forms present.
5. Faunal composition.

Abundance

The number of living foraminifera at any particular time should indicate the general level of organic production from estuary to estuary. Within one estuary, the abundance of foraminifera should point to local sources of energy supply. An estuary having very low standing crops, e.g. less than 10 specimens per 10 ml of wet sediment as in closed San Miguel Lagoon, Baja California (Stewart, 1958), is regarded as low in fertility and low in organic production. By contrast an estuary with relatively high standing crops, e.g. more than 1000 specimens per 10 ml as in the thin grass areas of Laguna Madre (Phleger, 1960b), has high organic production. Between these extremes, standing crop size alone is not an adequate index to fertility or to the rate of production. The growth rate and frequency of reproduction of a population need to be determined. Except for a few studies, i.e. Myers (1942) and Boltovskoy (1964), these factors remain to be determined in most areas.

Although foraminifera make up only a very small amount of the total benthos (less than 5% of metabolism, Horton, 1961) and less than one percent of the total bulk volume of sediment (except in some coral reefs they may make up more than five percent of the sediment) they are often abundant in areas where food supply or plant nutrients are abundant. For example, large populations averaging 500 - 2,000 specimens per

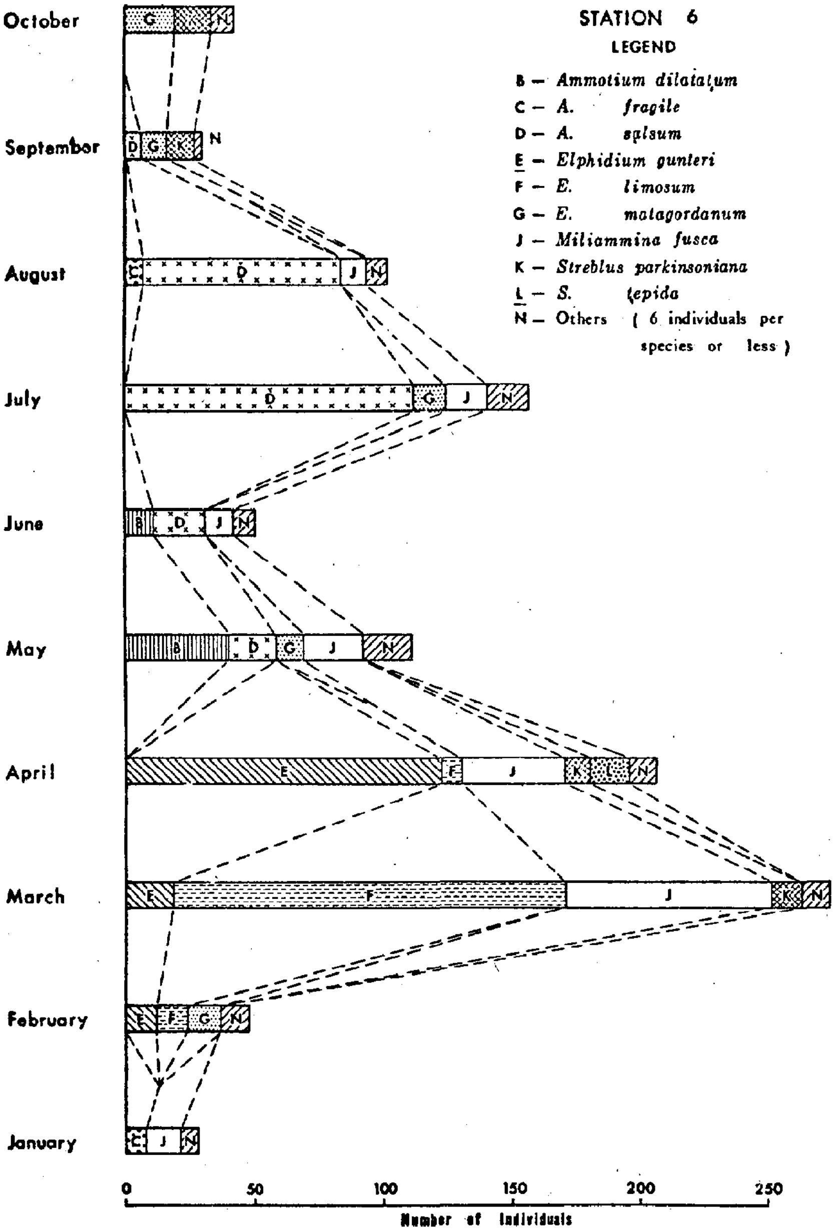


Fig. 1. Monthly distribution of foraminifera in Timbalier Bay, Louisiana. From Waldron (1963).

10 ml are recorded by Uchio (1960) off San Diego in an area of nutrient-rich upwelling. Populations of 1,500 to 3,000 per 10 ml occur off Main Pass of the Mississippi Delta and also off the Guadalupe River at the head of San Antonio Bay, Texas (Phleger, 1964), areas where river-borne nutrients are introduced and mixed with marine water (Fig. 2). Interestingly, the large populations are dominated by 1 - 4 species and specimens are typically of small size, features attributed to rapid reproduction of large populations under optimum conditions (Phleger, 1964). In the vicinity of the nutrient-rich Laguna Beach sewage outfall, California, Bandy et al. (1964c) found populations 5 times greater than elsewhere. These examples suggest that patterns of foraminiferal abundance point toward sources of organic input in an estuary.

Number of Species, Diversity and Dispersion

The relative number of species in a population, or species diversity, offers a useful means by which a population can be described. Recent studies (Gibson, 1966; Walton, 1964b) indicate the diversity is inversely proportional to the variability of the system. For example, the distribution of diversity in Mississippi Sound (Gibson, 1966) is relatively low (10 - 15 species) in areas of high wave and current activity or where salinity, temperature and turbidity are variable, whereas it is relatively high (25 - 40 species) in more stable water of the inner shelf (Fig. 3). Thus, diversity distributions of foraminifera are a means by which different habitats and different populations may be compared in terms of environmental variability.

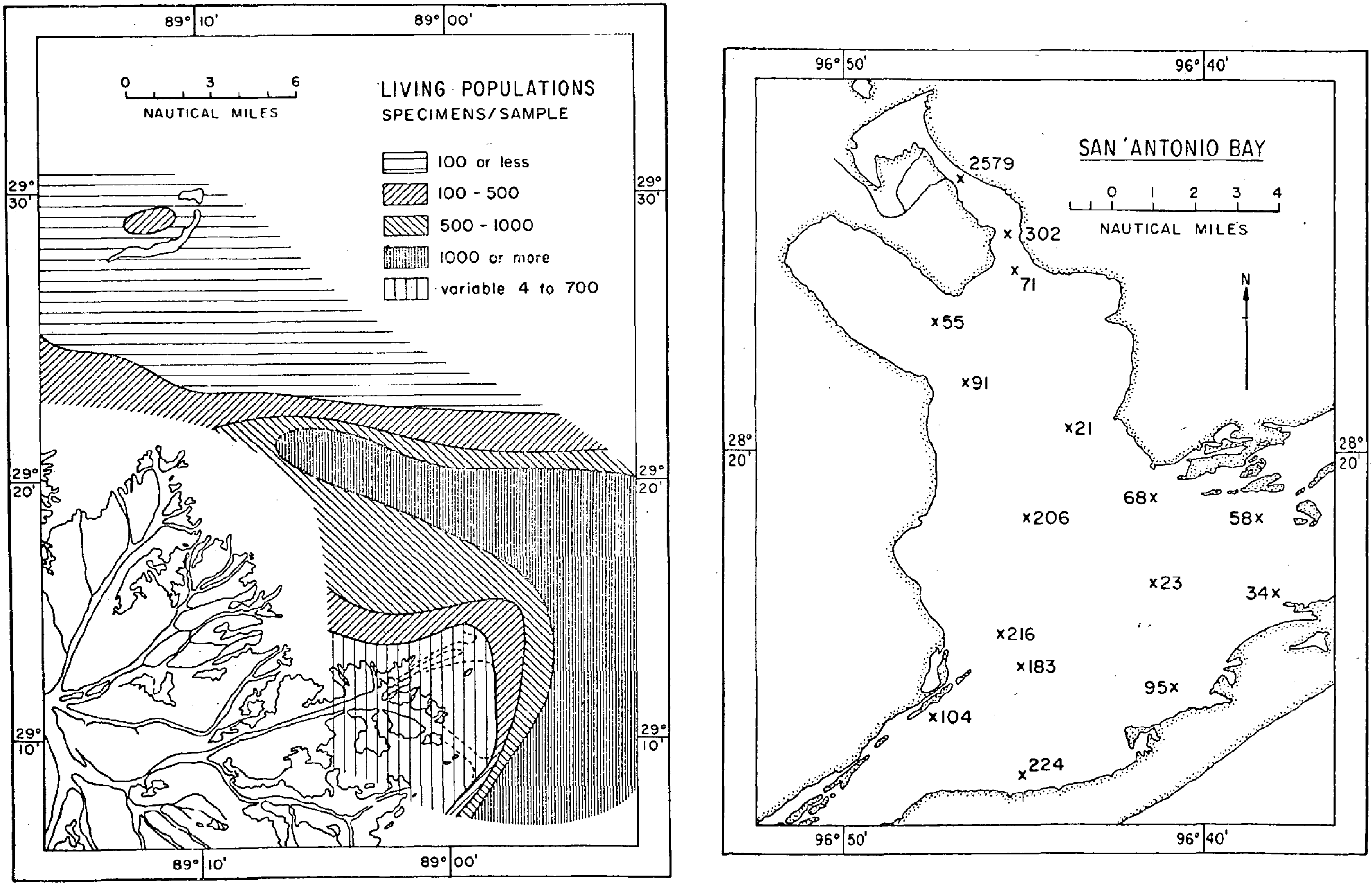
Closely related to species diversity is another characteristic, "faunal dominance," or the percentage occurrence of the most common species in a population (Walton, 1964b). Faunal dominance is directly proportional to environmental variability and inversely proportional to diversity. Varying from 90 percent in marshes to 20 percent on the continental shelf, it serves as a guide for examining broad trends in which rare species of nonindigenous species are present.

Like other estuarine populations, foraminifera are dispersed spatially in different patterns either random, uniform or clumped, according to their habit. The degree of clumping is a significant characteristic of a population but only a few studies have been made (Schafer, 1968b; Ellison, 1969; Lynts, 1966). In a study of spatial distributions in one square foot of Rehoboth Bay, Delaware, Buzas (1968b) observed an increase in aggregation with an increase in density random distributions were due to individuals settling out of water, whereas the abundant species were superimposed upon the random distribution as an aggregate due to asexual reproduction which produces a group of young about one parent.

Shell Characteristics and Composition

Foraminifera are often grouped according to the mode of their shell construction. These constructions appear to have environmental significance.

1. Arenaceous or agglutinate species build their tests of sand grains, mica flakes or other particles which they can cement together by carbonate or chitinous secretions. They occur in freshened or brackish water off river mouths and in partly confined estuaries where stagnant conditions often develop.


89° 10'
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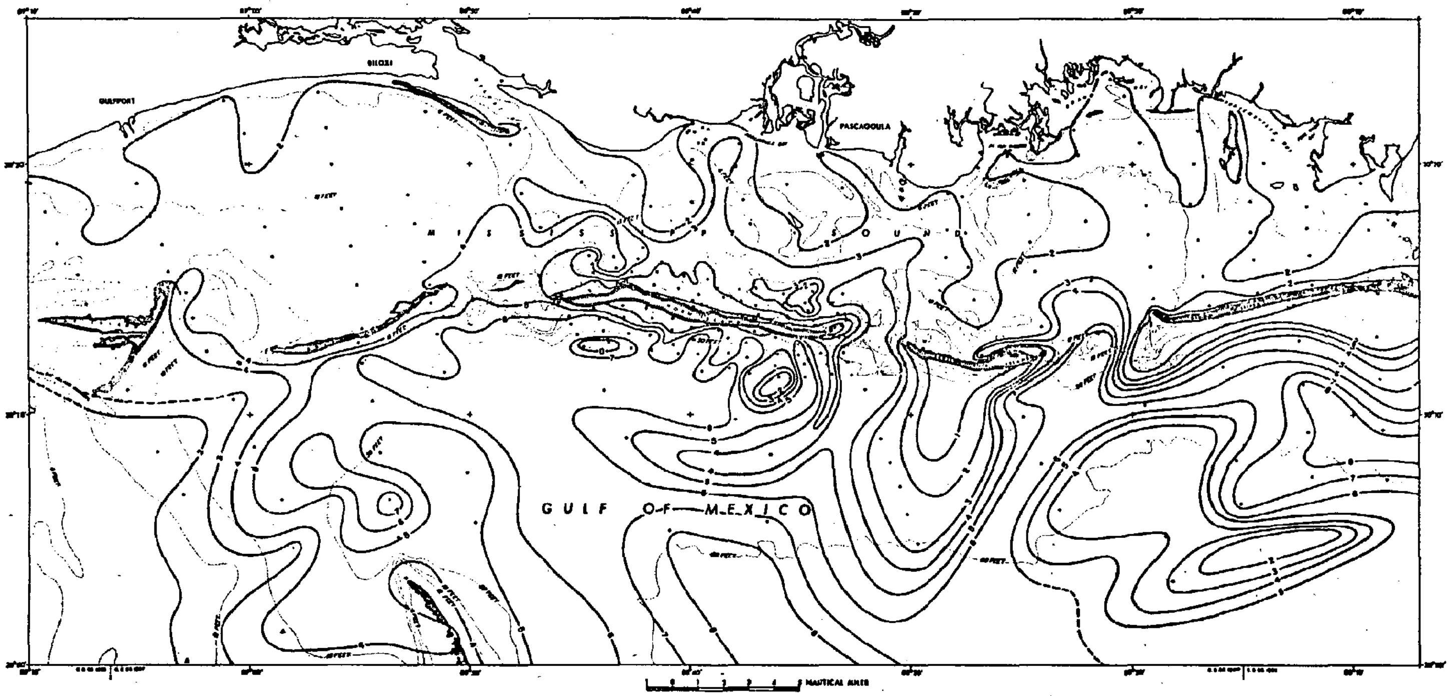
0 3 6
NAUTICAL MILES
LIVING POPULATIONS
SPECIMENS/SAMPLE
100 or less
100 - 500
500 - 1000
1000 or more
variable 4 to 700
29° 30'
29° 20'
29° 10'
96° 50'
96° 40'
SAN ANTONIO BAY
0 1 2 3 4
NAUTICAL MILES
N
28° 20'
2579
302
71
55
91
21
68
58
206
23
34
216
183
95
104
224

Fig. 2. Standing crops of benthonic foraminifera in southeast Mississippi delta (left), from Lankford (1959) and in San Antonio Bay, Texas (right), from Phleger (1964).


GULFPORT
BILOXI
PASCAGOULA
M I S S I S S I P P I S O U N D
G U L F O F M E X I C O
NAUTICAL MILES

DIVERSITY DISTRIBUTIONS, MISSISSIPPI SOUND AREA, VALUES CALCULATED
FROM PHLEGER, 1954, PARKER, 1954 TREADWELL, 1955.

- • PHLEGER, 1954
- • PARKER, 1954
- ▲ TREADWELL 1955

Fig. 3. Diversity distributions in Mississippi Sound, from Gibson (1966).

2. Calcareous species construct their tests of calcium carbonate secreted by the animal or precipitated from water. These are either porcelaneous (imperforate) or hyaline (perforate). Calcareous species mainly inhabit more marine water. Near sources of freshwater tests are commonly small and thin; some species (e.g. *Streblus beccarii* vars.) have chitinous inner linings.

When foraminifera grow in estuarine situations with high seasonal stress or pollution they often develop irregularly arranged chambers with contorted shapes at the apertural end. Abnormal specimens are reported by Arnal (1955) in Playa del Ray Lagoon, California, a confined and stagnant body of water, and by Stewart (1958) in closed San Miguel Lagoon, Baja California. They were found by Lidz (1965) around piers of Nantucket harbor. In landlocked Salton Sea, Arnal (1961) observed relatively high frequencies of abnormal specimens near the mouths of small streams. In laboratory cultures of Bradshaw (1955, 1957), chambers of *Streblus beccarii* became more irregular with an increase of temperature, a feature probably brought about by scarcity of food with increased metabolism of high temperatures.

Planktonic Forms

Although most foraminifera of estuaries inhabit the sediment surface a few attach themselves to rocks or plants and others are derived from ocean water masses. Planktonic forms, characteristic of offshore water masses, are often found together with nearshore benthonic forms where ocean water extends close to shore on an arid coast or in deep neutral embayments, e.g. San Pedro Bay, California (Bandy, 1964). When planktonic specimens are found in estuaries they may indicate occasional introduction of oceanic water.

Faunal Composition

Faunal composition when used together with other faunal characteristics provides a handle for comparing and classifying different estuaries. This is possible because estuarine foraminifera consist of characteristic species with dominant genera which have adapted in similar ways to similar conditions. Although the specific composition may differ or overlap somewhat from estuary to estuary, most groups are represented in many widely occurring estuaries from coast to coast. The change occurs mainly with distance seaward from fresh to marine water.

Thecamoebina fauna is characterized by small agglutinate forms that are close relatives of foraminifera but not classed as foraminifera. This group inhabits freshwater marshes, cypress swamps, bayous, lakes and rivers. Two common genera are *Difflugia* and *Centropyxis*. They are recorded in the lower Housatonic and Connecticut rivers (Parker, 1952), in the Guadalupe River, Texas (Parker *et al.*, 1953), and in the Mississippi Delta area (Walton, 1964b). A detailed study of thecamoebina along river courses in Trinidad by Todd and

Bronnimann (1957), indicates that different species occur in different river subsystems, or "zones."

A *Miliammina fauna* inhabits slightly salty water at the beginning of marine influence. This fauna is arenaceous and often includes species of *Ammoastuta*, *Trochammina* and *Haplophragmoides*, all of which also inhabit bordering intertidal marshes. In some areas this fauna often grades into, or is replaced by, a dominant *Ammobaculites* fauna.

An *Ammobaculites fauna* is common to inner or central parts of estuaries having intermediate salinity. In middle latitude estuaries it often makes up the main component of maximum populations off river mouths; diversity is relatively low. Lowman (1949) noted that shoal brackish waters which are occasionally stagnant are more prone to development of an arenaceous fauna than well-aerated waters. Seaward in more marine water of lower estuarine reaches, the *Ammobaculites* fauna is replaced by a calcareous *Elphidium* fauna. The change from arenaceous to calcareous character is a marked feature of estuarine faunas. It may reflect the availability of calcium carbonate used for test construction (Greiner, 1968), a feature which in turn depends on salinity, temperature, pH and the supply of river-borne calcium.

The *Elphidium fauna* is a more diverse group than the *Ammobaculites* fauna. It includes many species of *Elphidium* plus *Streblus* and miliolids. It inhabits lower estuarine reaches bathed by relatively salty water and penetrates landward in channels or through wide inlets which allow invasion of ocean water.

A *Miliolid fauna* is intermittently present in estuary entrances, adjacent barrier beaches and nearshore bottoms where turbulence is great. Specimens are robust, thick-shelled typically porcelaneous and relatively diverse. Added to the fauna are representatives from the *Elphidium* and *Streblus* faunas.

The *Streblus fauna* is a relatively widespread transitional fauna extending offshore to about the 60-foot depth. It often intergrades or overlaps the *Elphidium* fauna around estuary entrances and has a relatively high diversity.

Mixed faunas occur in migrating subsystems, around river and inlet entrances where currents are active in transporting tests and sediment. For example, thecamoebinids are often swept into the *Miliammina* or *Ammobaculites fauna* by river floods or freshets. Similarly marsh specimens may "contaminate" different estuarine faunas when eroded from bordering banks by wave action. Mixing can be recognized by the sparseness of living representatives, departures in the distribution of living dead faunal boundaries and local increases of diversity.

HORIZONTAL PATTERNS

The most distinctive patterns of estuarine foraminifera are those which occur with distance seaward. In temperate estuaries this pattern corresponds to a change from fresh to marine water but in estuaries of arid coasts the change is from hypersaline to normal marine. The broad horizontal patterns in temperate estuaries consist of:

1. A seaward change in faunal composition from dominately thecamoebinids in freshwater to arenaceous Miliammina or Ammobaculites in brackish inner reaches, and farther seaward to calcareous Elphidium, miliolids and Streblus (e.g. Fig. 4).

2. A seaward increase in the number of species as more marine and stable conditions are approached, e.g. from less than 10 to more than 25 species. There is a decrease in faunal dominance from about 90 to 30 percent (based on percent occurrence of the most dominant species).

3. Large populations occur near the effluence of rivers or inner reaches of estuaries, i.e. sites where nutrients are introduced into marine water and where salinity stress is high. Numbers diminish both landward as well as seaward, away from the loci of peak abundance.

4. Arenaceous forms, or calcareous forms with chitinous inner linings, dominant near river and inner estuarine reaches, in contrast to calcareous forms in lower reaches. Calcareous tests become smaller and thinner near sources of fresh water (Walton, 1964b).

5. Marsh forms contaminate inner reaches where marshes border an estuary. A few planktonic specimens may occur where ocean water approaches mouths of deep estuaries or invades embayments.

These broad patterns develop different dimensions according to the estuarine configuration, the degree of river dilution and mixing, and the magnitude of environmental stress. For example, Walton (1964a) observed that the Elphidium-Streblus fauna, which was so widespread throughout the relatively saline water of Tampa Bay, could not withstand the extreme dilution of inner Mobile Bay. In the Rappahannock River, Virginia, the thecamoebinid-Ammobaculites-Elphidium faunas extend through a broad gradient of salinity for a distance of 50 miles (Nichols and Ellison, 1967) whereas in the Yaquina estuary, Oregon, essentially the same faunas are telescoped into a narrow salinity gradient less than 10 miles long (Manske, 1968). In San Antonio Bay the bay facies dominated by Elphidium, spreads out over a broad area of the lower bay (Phleger, 1960), whereas in the Rappahannock estuary a similar fauna penetrates landward in a narrow zone of the estuary channel (Nichols and Ellison, 1967), (Fig. 5). In the James Estuary, Virginia, patterns of the Ammobaculites-Elphidium faunal boundary are skewed diagonally across the estuary in a way that suggests a response to Coriolis force manifest in the estuarine circulation and/or salinity distribution (Fig. 6).

Horizontal patterns may be expected to shift and alternate with changes in energy source and magnitude of stress. The Yaquina estuary, Oregon, alternates from well-mixed to partly-mixed with a change from high river inflow in winter and spring to low runoff and nearshore upwelling in summer. Foraminifera patterns recorded by Manske (1968) shift either upstream or downstream in response to these changes (Fig. 7). In the Rappahannock Estuary, Virginia, which has less intense seasonal stress and a wider salinity gradient than the Yaquina, faunal patterns also shift along the estuary with changes of salinity and river inflow (Ellison and Nichols, 1970), (Fig. 8). Both estuaries have similar dominant faunas but in the Yaquina there are more than 30 species whereas in the Rappahannock there are 21.

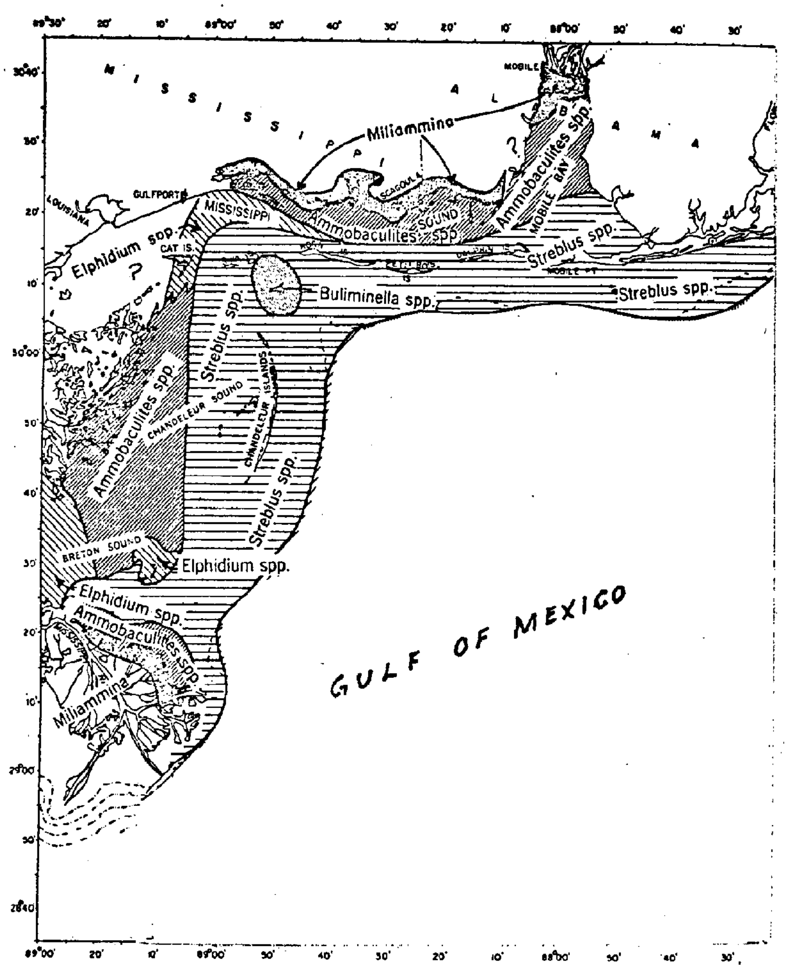

MISSISSIPPI
ALABAMA
MOBILE
Miliammina
Ammobaculites spp.
MOBILE BAY
GULFPORT
LOUISIANA
MISSISSIPPI SOUND
Ammobaculites spp.
CAT IS.
Elphidium spp.
Streblus spp.
Buliminella spp.
Streblus spp.
Streblus spp.
CHANDELEUR SOUND
CHANDELEUR ISLANDS
Ammobaculites spp.
Streblus spp.
BRETON SOUND
Elphidium spp.
Elphidium spp.
Ammobaculites spp.
Miliammina
GULF OF MEXICO

Fig. 4. Seaward change of principal foraminiferal faunas on the Gulf coast, Louisiana to Florida **(Modified from Walton, 1964b).**

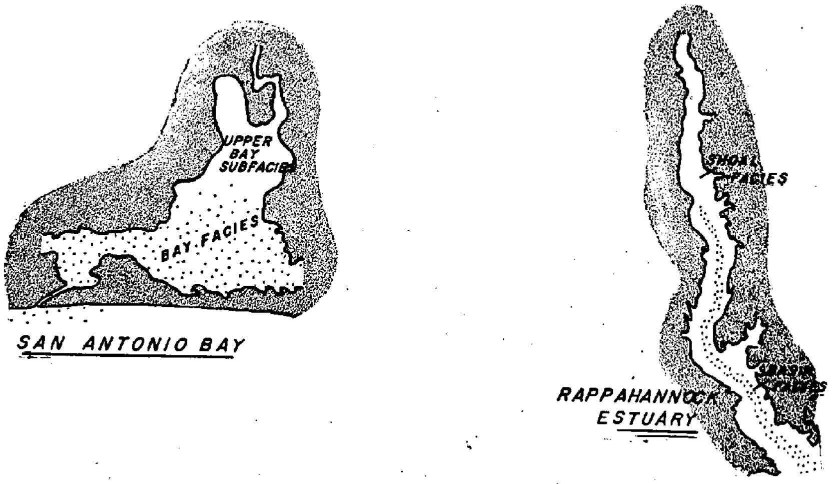

UPPER BAY SUBFACIES
BAY FACIES
SAN ANTONIO BAY
SHOAL FACIES
RAPPAHANNOCK ESTUARY

Fig. 5. Comparison of faunal patterns in a well-mixed shallow bay, San Antonio Bay, Texas, and a partly stratified river estuary, Rappahannock Estuary, Virginia, from Nichols and Ellison **(1967).**

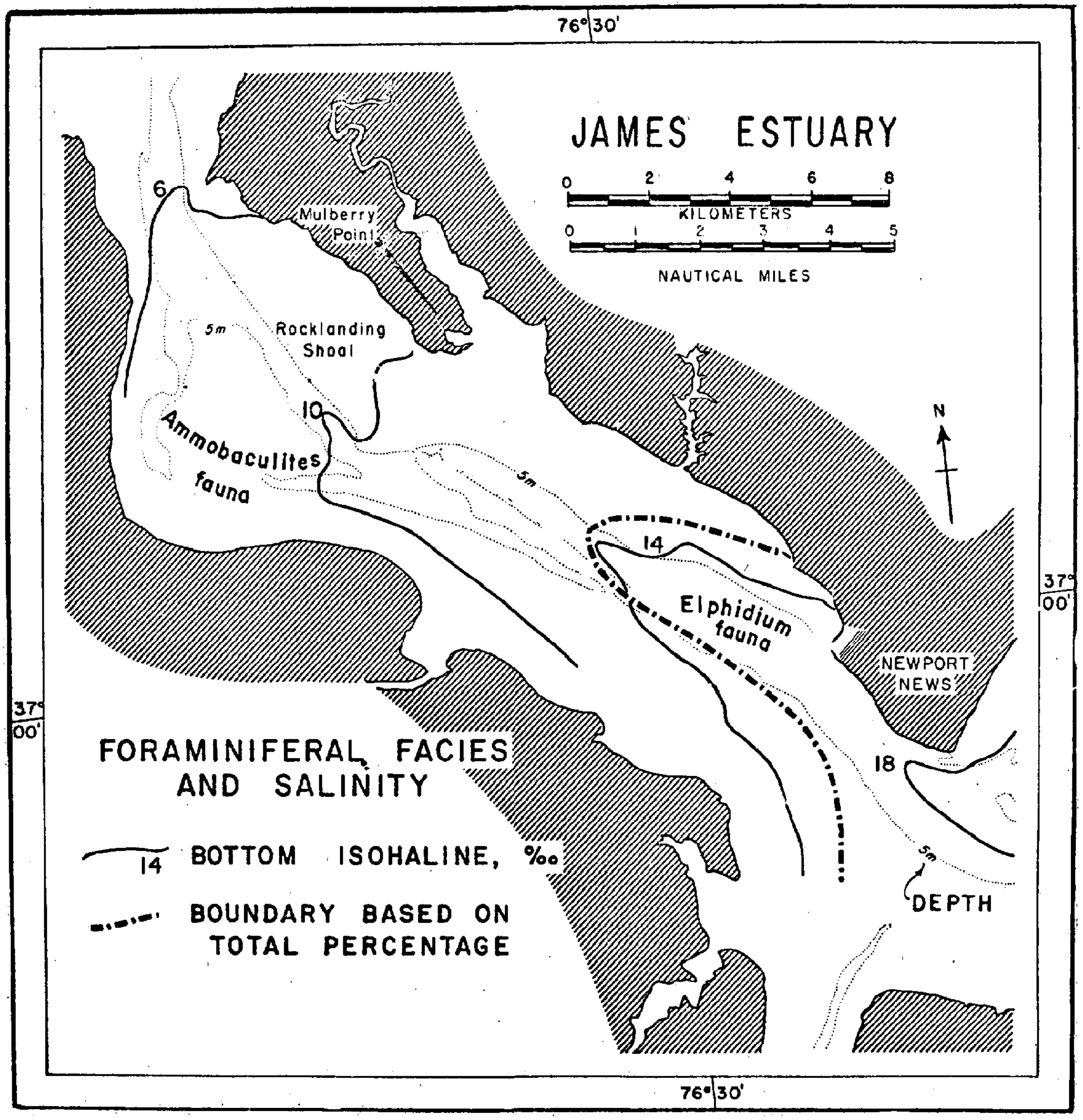

76°30'
JAMES ESTUARY
0 2 4 6 8
KILOMETERS
0 1 2 3 4 5
NAUTICAL MILES
6
Mulberry Point
5m
Rocklanding Shoal
10
Ammobaculites fauna
5m
14
Elphidium fauna
N
37° 00'
NEWPORT NEWS
18
5m
DEPTH
FORAMINIFERAL FACIES AND SALINITY
14 BOTTOM ISOHALINE, ‰
BOUNDARY BASED ON TOTAL PERCENTAGE
37° 00'
76°30'

Fig. 6. Ammobaculites-Elphidium faunal boundary in the James Estuary, Virginia (From Nichols and Norton, 1967).

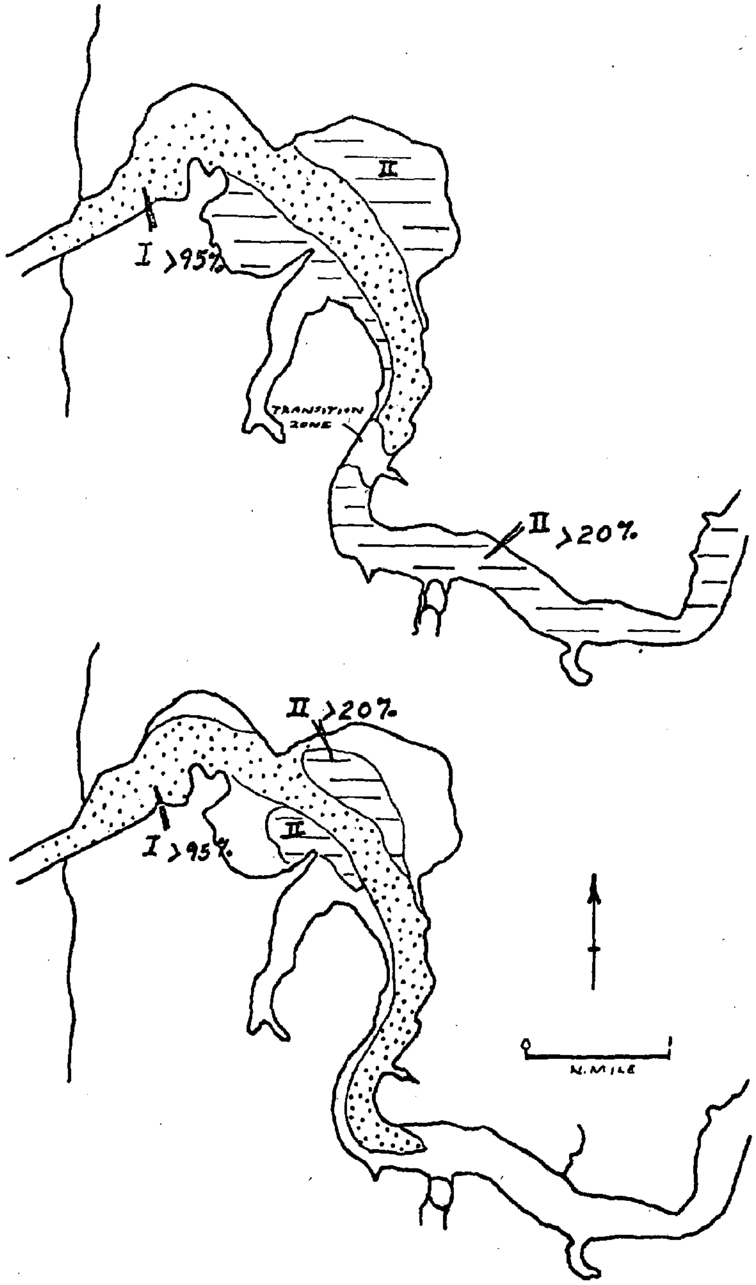

II
I >95%
TRANSITION ZONE
II >20%
II >20%
II
I >95%
0
1
N. MILE

Fig. 7. Distribution of principal foraminifera zones in Yaquina Bay, Oregon, upper, winter; lower, summer **(Modified from Manske, 1968).**

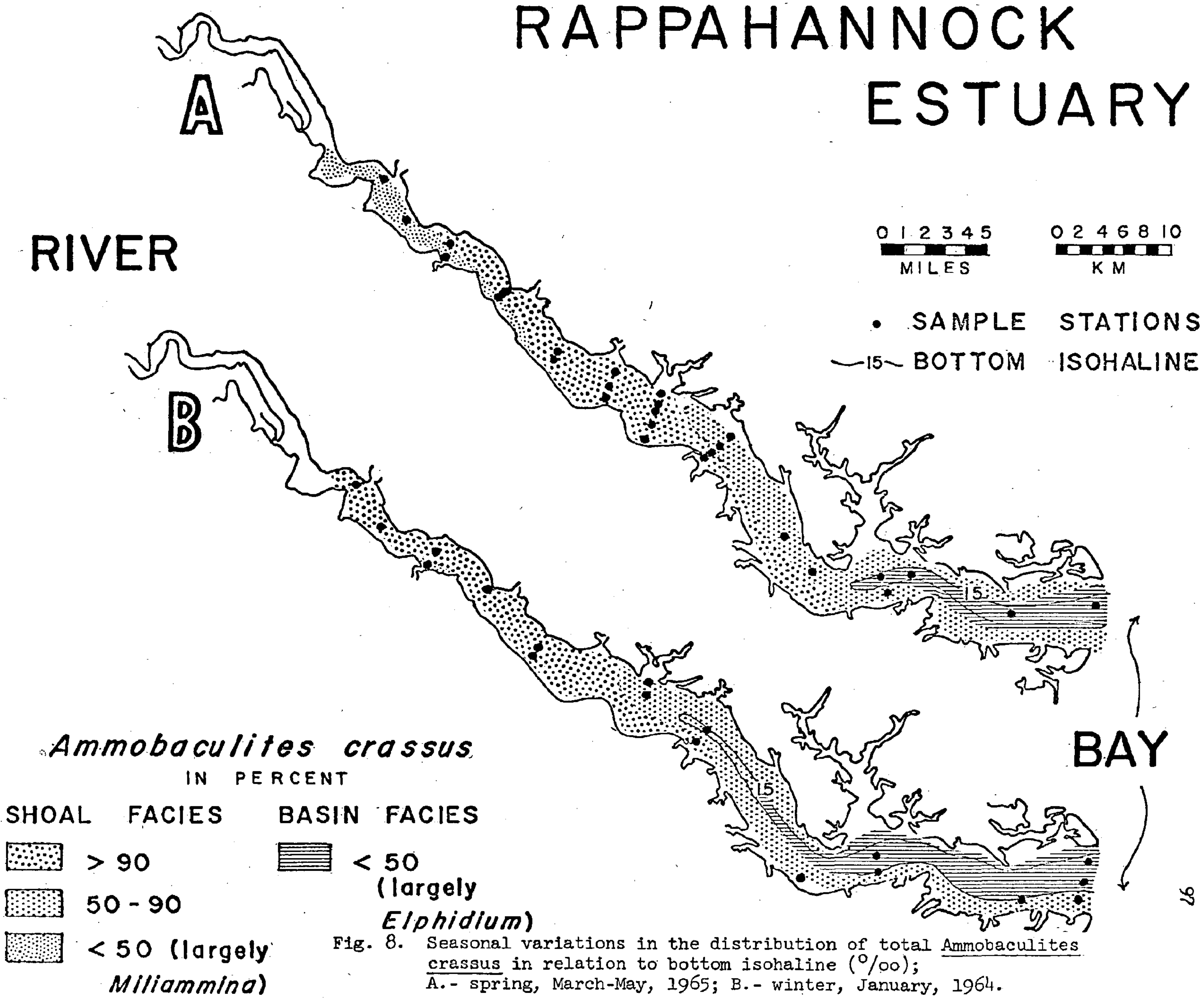

RAPPAHANNOCK
ESTUARY
A
B
RIVER
BAY
0 1 2 3 4 5
MILES
0 2 4 6 8 10
KM
• SAMPLE STATIONS
—15— BOTTOM ISOHALINE
15
Ammobaculites crassus
IN PERCENT
SHOAL FACIES
> 90
50 - 90
< 50 (largely *Miliammina*)
BASIN FACIES
< 50 (largely *Elphidium*)

Fig. 8. Seasonal variations in the distribution of total Ammobaculites crassus in relation to bottom isohaline (°/oo); A.- spring, March-May, 1965; B.- winter, January, 1964.

VERTICAL PATTERNS

Superimposed on the horizontal patterns there are smaller, less striking patterns with depth channelward or with elevation across flats. Vertical patterns are most conspicuous in intertidal zones of flats and marsh backed by freshwater ponds. They may also occur in deep estuaries, fjords and open embayments that merge with the continental shelf. Less striking are those that develop in shallow confined estuaries nearly cut off from the sea. For example, in Sabine Lake, Texas-Louisiana, shoals are inhabited by a Haplophragmoides Miliammina fauna whereas lower parts of the estuary floor are occupied by Ammobaculites (Fig. 9), (Kane, 1967). On shoals of Laguna Madre, great numbers of miliolids, up to 1640 living specimens per 10 ml, reflect high production on the lighted thin-grass shoals (Phleger, 1960c; and Odum and Wilson, 1962). Distributions of marsh foraminifera around Galveston Bay, Texas, (Phleger, 1960) display seven sub-zones that are partly related to plant zonation and other variables as tidal flooding, salinity, etc., all of which vary more-or-less with elevation. In the deep Juan de Fuca and Georgia Straits of the Pacific northwest, Cockbain (1963) differentiated 9 sub-zones, some of which varied with depth or related factors. Interestingly, faunas that inhabit freshened inner reaches of an estuary, also occupy shoals of seaward reaches which are influenced by partly freshened water. This is illustrated in foraminiferal distributions of Yaquina Bay, Oregon (Manske, 1968), (Fig. 7).

CHARACTERISTICS OF FORAMINIFERA IN DIFFERENT SYSTEMS

High Energy Beaches

Specimens are large, robust and thick shelled. Small, fragile forms do not survive the intense turbulence and sorting action of wave action. Large Miliolidae, Elphidium and Streblus dominate faunas on the Gulf coast (Phleger, 1960c). On the Pacific coast Cooper (1961) found abundant hyaline specimens and relatively few species (averaging 15). On southern California beaches, Bandy (1963) reports abundant broken, damaged and worn specimens. Lankford (1962) delineated two faunal provinces in beach and nearshore areas along the Pacific coast with a boundary at Point Conception, California. Miliolids and Elphidium were limited to the southern California province. On the Atlantic coast at Martha's Vineyard, Todd and Low (1961) recorded variable numbers of Miliolids, species of Elphidium, Streblus and Rosaline. Presumably they were largely derived from seaward of the low tide line.

High Velocity Channels

Under conditions of strong currents, foraminifera are sparse and limited to minute or attached species. Todd and Low (1961) report flattened forms of the genera Rosalina and Cibicides in current washed inlets of Martha's Vineyard, Massachusetts. In tidal channels of Hadley Harbor, Massachusetts, known as "gutters," populations vary in abundance and species diversity (Buzas, 1968a). Channels leading into lagoons on the southern California coast contain beach species mixed with lagoon species (Bandy, 1963).

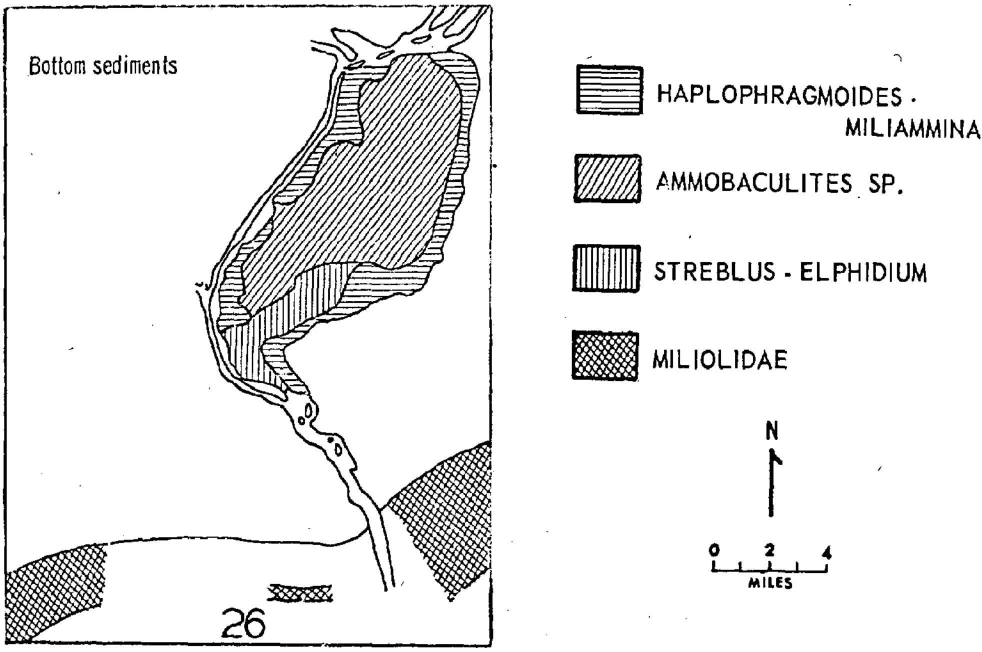

Bottom sediments
HAPLOPHRAGMOIDES - MILIAMMINA
AMMOBACULITES SP.
STREBLUS - ELPHIDIUM
MILIOLIDAE
N
0 2 4
MILES
26

Fig. 9. Foraminiferal patterns in Sabine Lake, Texas-Louisiana, from Kane (1967).

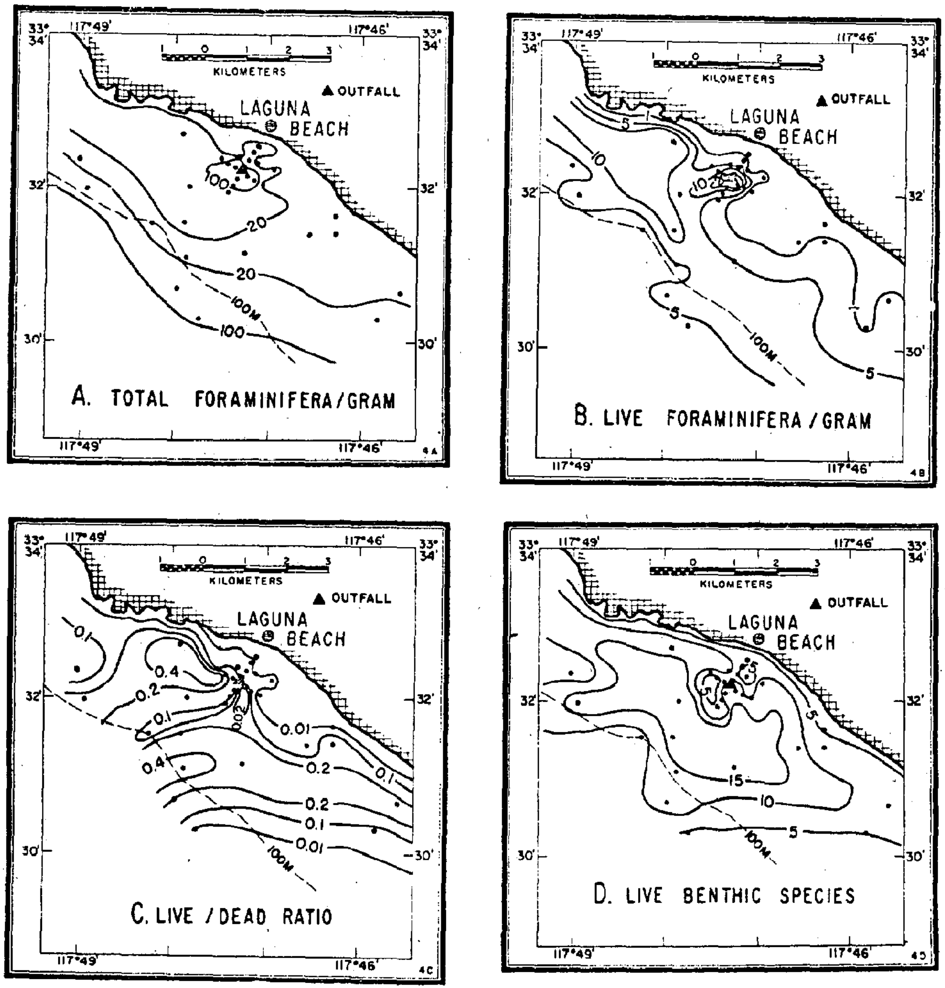

33° 34'
117°49'
117°46'
32'
30'
KILOMETERS
1 0 1 2 3
▲ OUTFALL
LAGUNA
BEACH
100
20
100M
A. TOTAL FORAMINIFERA/GRAM
10
5
B. LIVE FORAMINIFERA/GRAM
0.1
0.4
0.2
0.01
C. LIVE/DEAD RATIO
15
10
5
D. LIVE BENTHIC SPECIES

Fig. 10. Foraminiferal patterns around the Laguna Beach sewage outfall, from Bandy et. al. (1964c).

Sedimentary Deltas

Foraminiferal faunas are best illustrated by the studies of Lankford (1959, 1967a) on the southeast Mississippi delta (Fig. 2). The "fluvial marine" fauna of passes consists of abundant Palmerinella gardenislandensis, an arenaceous form. Seaward of the passes where river and gulf waters actively mix and where sedimentation is fast, the fauna is characterized by very high living populations dominated by 4 species of the genera Bolivina, Buliminella, Epistominella and Nonionella. A very different faunal composition is recorded by Phleger (1960a) off the Guadalupe River delta in inner San Antonio Bay, where there are abundant arenaceous Ammotium salsum and Palmerinella gardenislandensis plus species of calcareous Elphidium and Streblus. Because of rapid sedimentation, dead populations are "diluted" and the ratio of living to dead tests is high. Faunas of the two areas are similar in having large standing crops composed of only a few species.

Hypersaline Lagoons

Faunas described from Laguna Madre, Texas, by Phleger (1960c) are dominated by Miliolidae which inhabit sand substrates commonly covered with thin grass. In deeper areas of silt and clay, the fauna is dominated by species of Elphidium and Streblus; miliolids are less abundant. In turbid, poorly vegetated Baffin Bay, Texas, the fauna is impoverished and the number of species few (less than 7).

Blue-Green Algal Mat

Faunas on "matted" barrier flats of Laguna Madre are dominantly miliolids that occur in relatively large percentages. On an algal covered barrier flat of St. Joseph's Island, Texas, Phleger (1966b) recorded abundant miliolids plus species of Streblus, Elphidium and the arenaceous genus Ammotium. Species average about 15, a number slightly higher than in most surrounding marshes.

Mangroves

In the marsh-mangrove bay areas of Whitewater Bay and Ten Thousand Islands, Florida, Phleger (1966a) found dominantly calcareous species similar to those in lagoons of south Texas plus a few arenaceous "marsh" species. Populations are relatively large and fairly diverse, embracing about 20 species.

Tropical Meadows

The foraminiferal fauna of Florida Bay is characterized by abundant calcareous miliolids (Lynts, 1962). They tend to increase in abundance seaward toward more salty marine water, whereas Streblus beccarii and Elphidium galvestonense, the other principal components of the fauna, tend to decrease seaward away from freshened water near the mainland. Populations are very diverse, ranging up to 57 species for the whole area, and they also vary widely in abundance (Moore, 1957).

Blue Water Coasts

Blue waters bathing the southeast coast of Florida in depths of 0-40 feet, hold a more diverse fauna than in Florida Bay, consisting mainly of Peneroplidae and Miliolidae (Moore, 1957). Populations are variable owing in part to sorting by currents and waves.

Tide Pools

Foraminifera reported from algal-rimmed tide pools from Oregon and California by Cooper (1961) vary widely in abundance and in number of species, from 12 to 46. With distance from north to south the over-all number of species increase. Most forms are hyaline (those with perforate calcareous tests) but there are small percentages of arenaceous, and porcellaneous forms, in addition to a few distorted forms of Miliodidae and planktonic fossils. The fauna is believed to be indigenous to nearshore areas and swept into the pools by waves and currents.

Oyster Reefs

On oyster grounds of the inner James and Rappahannock estuaries, Virginia, foraminifera reach maximal numbers consisting of 1 to 3 arenaceous species, mainly Ammobaculites. It is not known if these faunal features are part of the oyster reef economy or part of the estuarine-wide economy. No casual relationship between foraminifera and oyster reefs has been reported even in the fairly detailed studies of oyster-rich Mobile Bay, San Antonio Bay (Phleger, 1960), and Matagorda Bay (Shenton, 1957; Lehman, 1957).

Marshes

Marsh faunas are very variable in composition and abundance. They are typically arenaceous, low in diversity (5 - 8 species) and appear to have a very wide distribution (Phleger, 1960b). Characteristic genera include Ammoastuta, Trochammina and Miliammina. Detailed studies have been made on the Texas coast by Phleger (1965, 1966b) on the Massachusetts coast by Phleger and Walton (1950) and by Todd and Low (1961) and on the southern California coast by Bandy (1963). They are often washed onto adjacent lagoon or estuary floors as "contaminants."

Oligohaline Systems

Foraminifera of the salinity "gradient" zone in the inner James and Rappahannock estuaries, Virginia, consist of very large populations of 1 to 3 species, mainly arenaceous forms dominated by one species, Ammobaculites. Populations averaging 225 specimens per 10 ml are larger than most medium-salinity plankton estuaries, but less than the very large populations off the Mississippi River. The fauna is partly contaminated with a few "marsh" species derived from upstream.

Medium-Salinity Plankton Estuary

Foraminifera of this type system are exemplified by those in Long Island, N. Y., reported by Buzas (1965). The entire fauna consists of 23 species with larger numbers toward more marine areas to the east. Calcareous species of Elphidium plus Buccella frigida and Eggerella advena, which constitute 90 percent of the total population, form three depth zones at depths of 36, 76 and 87 feet. Living populations average 177 per sample at depths of 30-60 feet and reach 335 per sample in shallow water 0 to 30 feet. Large populations occurring in October and June correlate in a general way with the zooplankton and phytoplankton cycles as well as times of maximum temperature.

Emerging Systems

There are few comprehensive studies of foraminifera in new man-made systems except those of sewage outfalls on the southern California coast studied by Bandy, Ingle and Resig (1964a,b,c, and 1965a). Both benthic and planktonic species reflect nutrient enrichment by their great abundance near the outfalls and by a reduction in species number (Fig. 10). On the Kennebec River estuary, Maine, toxic paper mill pollution led to low abundance and few species (Schafer and Sen Gupta, 1969). In Nantucket Harbor, Massachusetts, organic-rich muds exposed to sewage yielded an abundance of abnormal specimens (Lidz, 1965). On the other hand, an abundance of Florilus grateloupii and Fursenkoina pontoni is favored by sewage pollution in Mayaguez and Guayanilla Bays, Puerto Rico (Seiglie, 1968). McCrone and Shafer (1966) report Ammonia beccarii tolerates substantial pollution in the Hudson estuary. In a study of thermal pollution effects, Christensen and Ellison (1965) found high temperatures, up to 14°C above normal, have only limited effect on Ammobaculites. Additional studies are needed to determine how foraminifera respond to different man-made stresses.

PROBLEMS FOR FUTURE RESEARCH

Knowledge of foraminifera at present is not fully adequate to attack the multitude of future problems arising from pollution and conservation of water resources. Certain areas of understanding are deficient and require attention. The following are priority studies, though not listed in numerical order by priority, within reach of investigation with present tools and which hold promise of solution.

1. Although natural distributions of foraminifera are known from many systems they do not cover all estuarine types. They can serve as "base-line" information for evaluating future man-made changes before such changes occur. Distributional studies are needed in: (1) Glacial and turbidity outwash fjords, (2) ice stressed intertidal zones, (3) high energy beaches of the east coast, (4) oscillating temperature channels, (5) tropical "meadows," and (6) tropical plankton bays of Puerto Rico and Hawaii.

2. Emerging man-stressed systems have been little studied except for sewage outfalls in temperate neutral embayments and shore waters. Basic distribution studies are needed to compare patterns in different stressed systems at varying scales and intensities of stress, from the tropics to the Arctic. It is of special interest to know how foraminiferal populations respond to conditions in new systems as regards number of species, abundance, development of abnormalities, spatial variability, and diversity. How do distribution patterns shift in response to deepening, damming or diversion of an estuary?

3. To further our understanding of distributions in natural as well as man-stressed systems, more information is needed about the system itself, especially time series that show extremes, durations and rates of change of temperature, salinity, pH, current, light, oxygen suspended concentrations and other parameters. This information can be obtained from existing continuous recording instruments, such as developed by Bradshaw (1968) and further used for analysing the ecology of other organisms as well. Automatic processing and computer analysis should facilitate handling large amounts of data and analyses of various environmental variables as a group.

4. To refine our evaluation of distributional features we need to know how foraminiferal tests behave under turbulent conditions; and to what degree tests are passively transported and dispersed by tidal currents. Detailed analysis of foraminifera and of suspended sediment, supplemented by simulated conditions in laboratory flumes, will aid in this problem. Eventually, foraminifera may be of use in measuring the degree to which sediments are dispersed by turbulence and mixed by other organisms. They are potentially useful as a tracer of dredge spoil.

5. Like other marine organisms, foraminifera are capable of concentrating trace elements including those of man-made wastes. Inasmuch as the trace composition is little known, analyses need to be made to determine what elements are concentrated by different species and how they may affect the size and survival of entire populations.

6. Of special import is the need to relate the production of foraminifera to total organic production. If a relationship can be developed, foraminifera could be used as an index for recognizing productive estuaries and for comparing organic production rates with time or in different systems.

Part III-A

ECOLOGICAL SYSTEMS BY STATE

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In the same sense that maps of geological formations, soils, forests, and agricultural use are the basis for management of systems of man and nature on land, detailed maps of the ecological systems of the coastal waters are needed. In some states there are already detailed maps showing shellfish locations, bacterial pollution, salinities, and other related properties, but not maps of the whole operating ecological systems as defined in Part I. Most states have the personnel to do this mapping in a relatively short time because of knowledge accumulated already in management and scientific studies of the bays. When accomplished, the detailed maps may become the basis for management of the coastal systems of America, especially as our knowledge of the types develops further.

For consideration of the national estuarine resource, some small scale maps that locate a few examples of each type of ecosystem in each state are given to help readers visualize the system types in the ecology of these states. In this chapter, using the maps, we list examples of ecosystem types obtained in interviews in each state. A number of state authorities have indicated their disappointment that these small maps show so little of the detail already known locally, thus underscoring our recommendations that the detailed and documented resource maps be done by ecosystem type as a national project with state-federal collaboration. This volume, however, is written to lead non-scientists into the estuarine literature. The small maps are presented in the belief that basic concepts must be first introduced in simplified form. We seek to show readers new to estuarine science some examples of locations of ecological systems, to show readers familiar with one state the characteristics of another, and to show the kind of mapping approach that might be followed in doing detailed large maps of the same areas. The maps also show locations of the estuaries discussed in the chapters that follow.

Lest there be misuse of these introductions we pass on a caution from one of our correspondents quoted as follows:

> ". . . what needs emphasis is that we have almost none of the hard, detailed information which is needed to intelligently manage most of our shore areas. Written material like this is likely to give would-be managers the illusion that they know a whole lot, and can now proceed with safely predictable results. It seems to me this could lead to great damage. What these managers really need is a brochure setting out the complexity of the problems to be faced, and pointing out the necessity of making detailed local studies of each particular situation before making drastic changes therein."

Within each geographical area there may be several systems and subsystems in juxtaposition with each other. A large bay, for example, may be surrounded by marshes, tidal pools and mudflats and contain in it an oligohaline system, medium salinity plankton system, oyster reefs, grass bottoms, and migrating subsystems. Thus, the classification of one large bay may be difficult and complex because of the necessity of all these systems and subsystems interacting together to provide the productivity characteristic of that bay. You may find, therefore, many classification designations within one small area, such as Chesapeake Bay, Pamlico Sound, Galveston Bay, or San Francisco Bay, to name a few.

Maps are alphabetically arranged by state except for Alabama in Fig. 3; Connecticut in Fig. 9; Delaware in Fig. 8; Mississippi in Fig. 6; New Hampshire in Fig. 7; Rhode Island in Fig. 9; and Virginia in Fig. 8. We acknowledge the suggestions of many in the states.

Figure 18 (U. S. Federal Water Pollution Control Administration, 1967 1) is a more detailed mapping of only one ecological system (sea food waste) in the estuaries of a single state. It illustrates the difficulty, but also the potential usefulness, of such mapping.

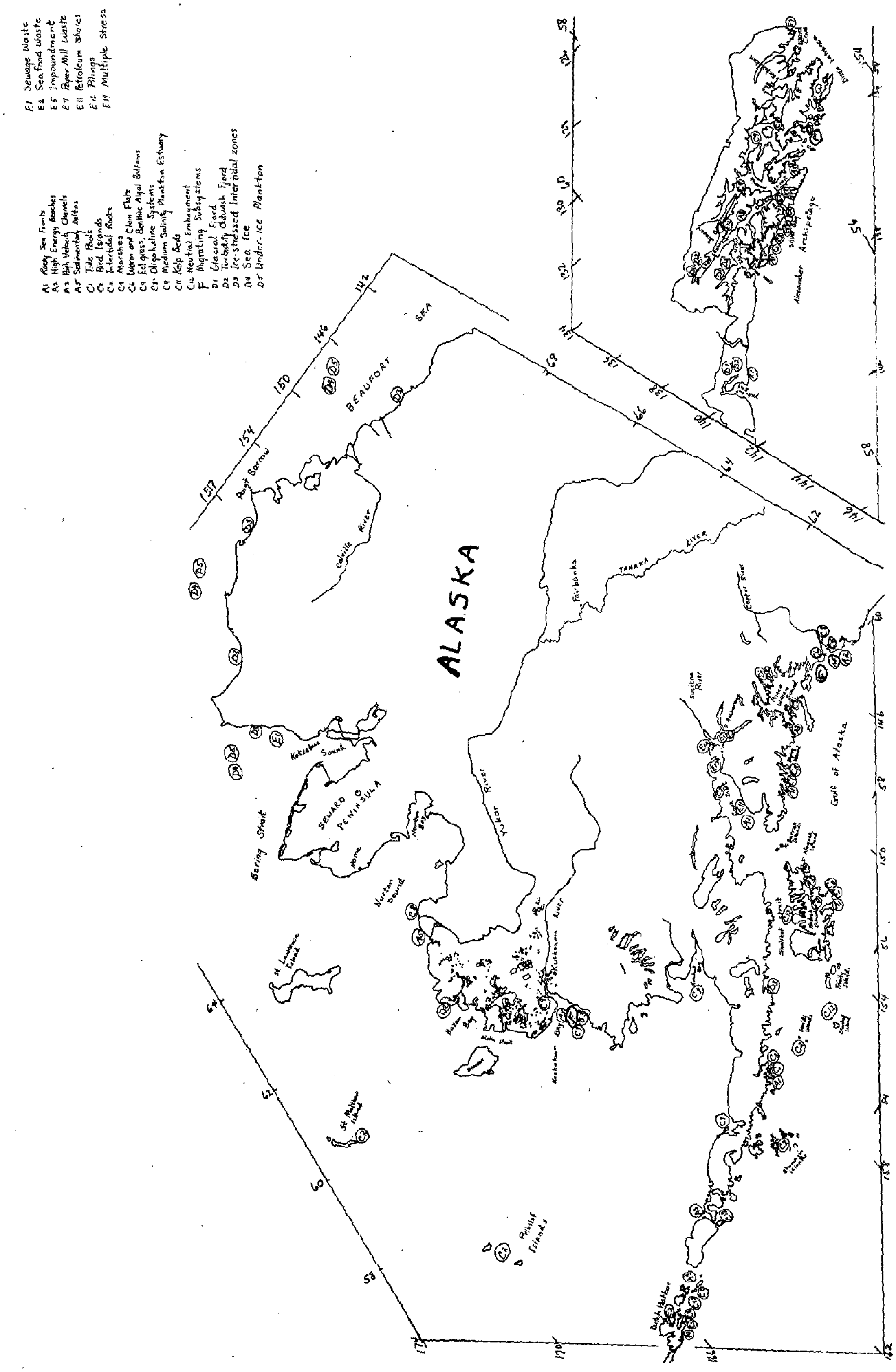

A1 Rocky Sea Fronts
A2 High Energy Beaches
A3 High Velocity Channels
A5 Sedimentary Deltas
C1 Tide Pools
C2 Bird Islands
C3 Intertidal Rocks
C4 Marshes
C6 Worm and Clam Flats
C7 Eel grass, Benthic Algal Bottoms
C8 Oligohaline Systems
C9 Medium Salinity Plankton Estuary
C11 Kelp Beds
C12 Neutral Embayment
F Migrating Subsystems
D1 Glacial Fjord
D2 Turbidity Outwash Fjord
D3 Ice-stressed Intertidal zones
D4 Sea Ice
D5 Under-ice Plankton
E1 Sewage Waste
E2 Seafood Waste
E5 Impoundment
E7 Paper Mill Waste
E11 Petroleum Shores
E12 Pilings
E19 Multiple Stress
ALASKA
BEAUFORT SEA
Point Barrow
Colville River
Fairbanks
TANANA RIVER
Yukon River
Kotzebue Sound
SEWARD PENINSULA
Bering Strait
Nome
Norton Sound
St. Lawrence Island
St. Matthew Island
Pribilof Islands
Kuskokwim River
Hazen Bay
Kuskokwim Bay
Copper River
Susitna River
Gulf of Alaska
Shelikof Strait
Dutch Harbor
Alexander Archipelago
158
154
150
146
142
64
62
60
58
56
54
170
166
162
138
134
130

Fig. 1. Alaska

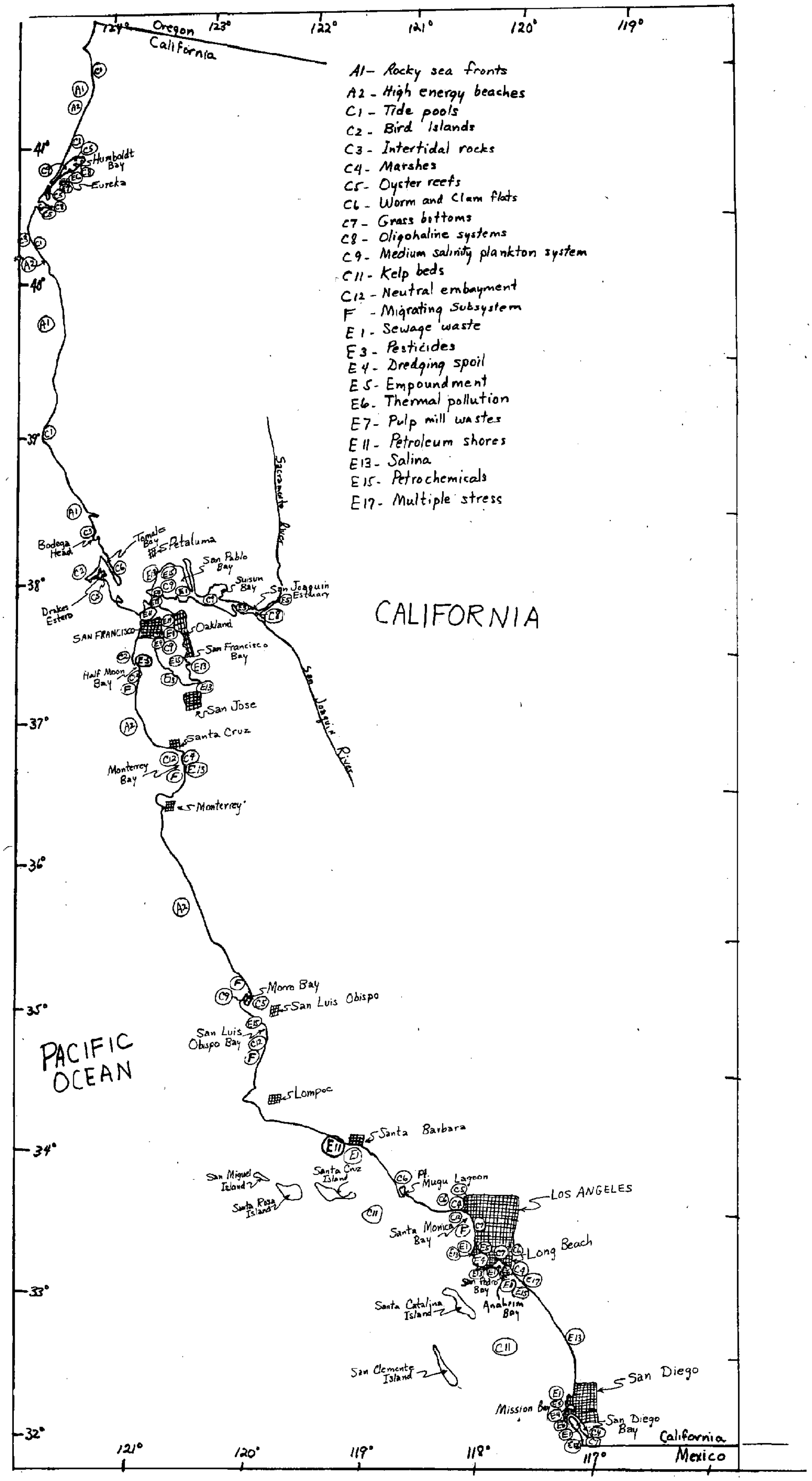

124°
Oregon
California
123°
122°
121°
120°
119°
A1- Rocky sea fronts
A2 - High energy beaches
C1 - Tide pools
C2 - Bird Islands
C3 - Intertidal rocks
C4 - Marshes
C5 - Oyster reefs
C6 - Worm and Clam flats
C7 - Grass bottoms
C8 - Oligohaline systems
C9 - Medium salinity plankton system
C11 - Kelp beds
C12 - Neutral embayment
F - Migrating Subsystem
E1 - Sewage waste
E3 - Pesticides
E4 - Dredging spoil
E5 - Empoundment
E6 - Thermal pollution
E7 - Pulp mill wastes
E11 - Petroleum shores
E13 - Salina
E15 - Petrochemicals
E17 - Multiple stress
41°
Humboldt Bay
Eureka
40°
39°
Bodega Head
Tomales Bay
Petaluma
San Pablo Bay
Suisun Bay
San Joaquin Estuary
Sacramento River
38°
Drakes Estero
SAN FRANCISCO
Oakland
San Francisco Bay
Half Moon Bay
San Jose
San Joaquin River
CALIFORNIA
37°
Santa Cruz
Monterey Bay
Monterey
36°
Morro Bay
San Luis Obispo
35°
San Luis Obispo Bay
PACIFIC OCEAN
Lompoc
Santa Barbara
34°
San Miguel Island
Santa Cruz Island
Santa Rosa Island
Pt. Mugu Lagoon
LOS ANGELES
Santa Monica Bay
Long Beach
33°
San Pedro Bay
Santa Catalina Island
Anaheim Bay
San Clemente Island
San Diego
Mission Bay
San Diego Bay
32°
California
Mexico
121°
120°
119°
118°
117°

Fig 2. California

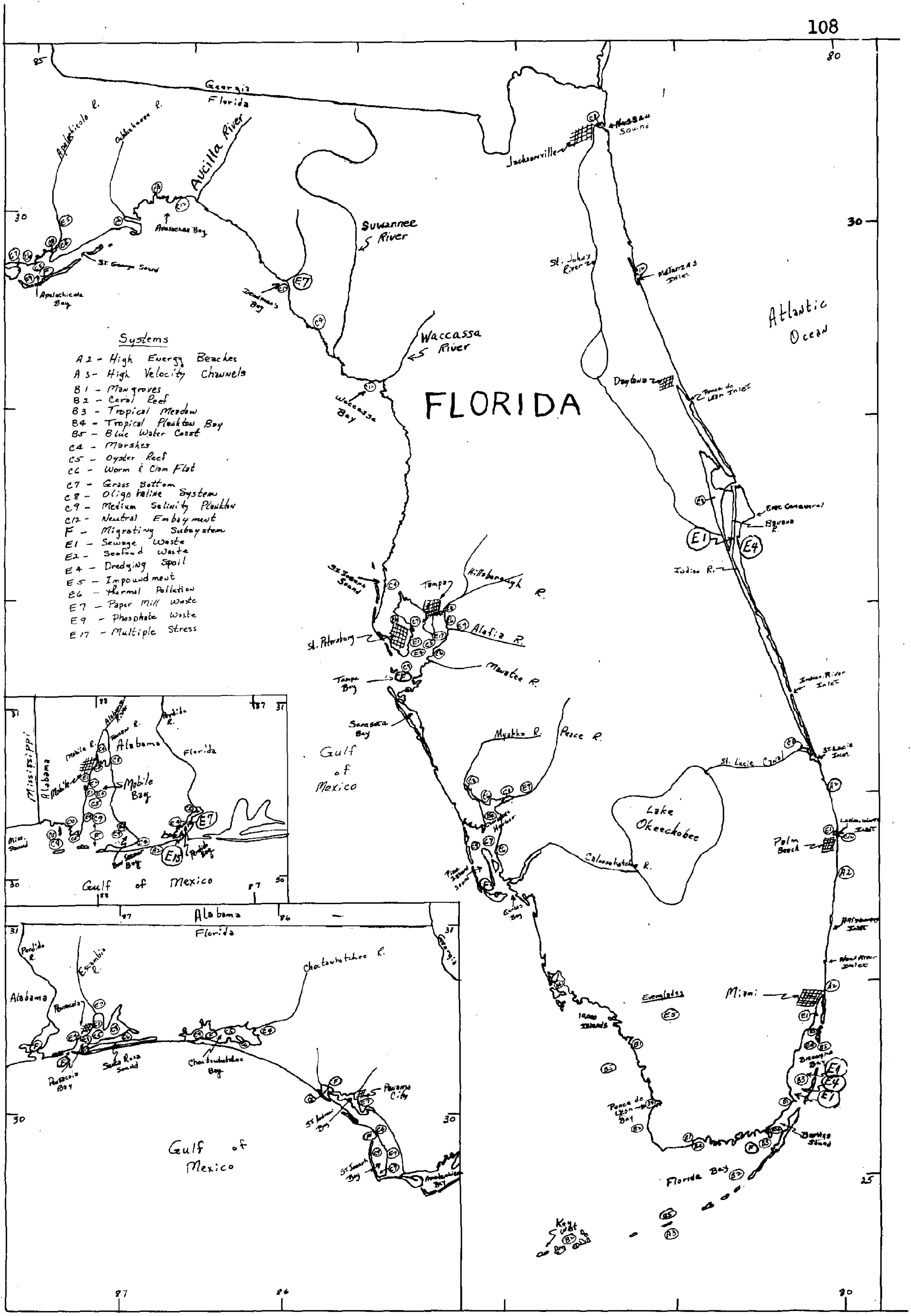

Systems
A 2 - High Energy Beaches
A 3 - High Velocity Channels
B 1 - Mangroves
B 2 - Coral Reef
B 3 - Tropical Meadow
B4 - Tropical Plankton Bay
B5 - Blue Water Coast
C4 - Marshes
C5 - Oyster Reef
C6 - Worm & Clam Flat
C7 - Grass Bottom
C8 - Oligohaline System
C9 - Medium Salinity Plankton
C12 - Neutral Embayment
F - Migrating Subsystem
E1 - Sewage Waste
E2 - Seafood Waste
E4 - Dredging Spoil
E5 - Impoundment
E6 - thermal Pollution
E7 - Paper Mill Waste
E9 - Phosphate Waste
E17 - Multiple Stress
FLORIDA
Georgia
Florida
Apalachicola R.
Ochlockonee R.
Aucilla River
Apalachee Bay
St. George Sound
Apalachicola Bay
Suwannee River
Deadman's Bay
Waccassa River
Waccassa Bay
Jacksonville
Nassau Sound
St. John's River
Matanzas Inlet
Atlantic Ocean
Daytona
Ponce de Leon Inlet
Cape Canaveral
Banana R.
Indian R.
E1
E4
St. Joseph Sound
Tampa
Hillsborough R.
Alafia R.
St. Petersburg
Manatee R.
Tampa Bay
Sarasota Bay
Gulf of Mexico
Myakka R.
Peace R.
Charlotte Harbor
Pine Island Sound
Estero Bay
Caloosahatchee R.
Lake Okeechobee
St. Lucie Canal
St. Lucie Inlet
Indian River Inlet
Lake Worth Inlet
Palm Beach
Hillsboro Inlet
New River Inlet
Miami
Everglades
E5
10,000 Islands
Ponce de Leon Bay
Biscayne Bay
Barnes Sound
Florida Bay
Key West
30
25
80
85
Mississippi
Alabama
Mobile R.
Tensaw R.
Alabama River
Perdido R.
Mobile
Mobile Bay
Miss. Sound
Bon Secour Bay
Perdido Bay
E15
E7
Gulf of Mexico
31
30
88
87
Alabama
Florida
Perdido R.
Escambia R.
Pensacola
Pensacola Bay
Santa Rosa Sound
Choctawhatchee R.
Choctawhatchee Bay
Panama City
St. Andrews Bay
St. Joseph Bay
Apalachicola Bay
Georgia
Gulf of Mexico
87
86

Fig. 3. Florida and Alabama

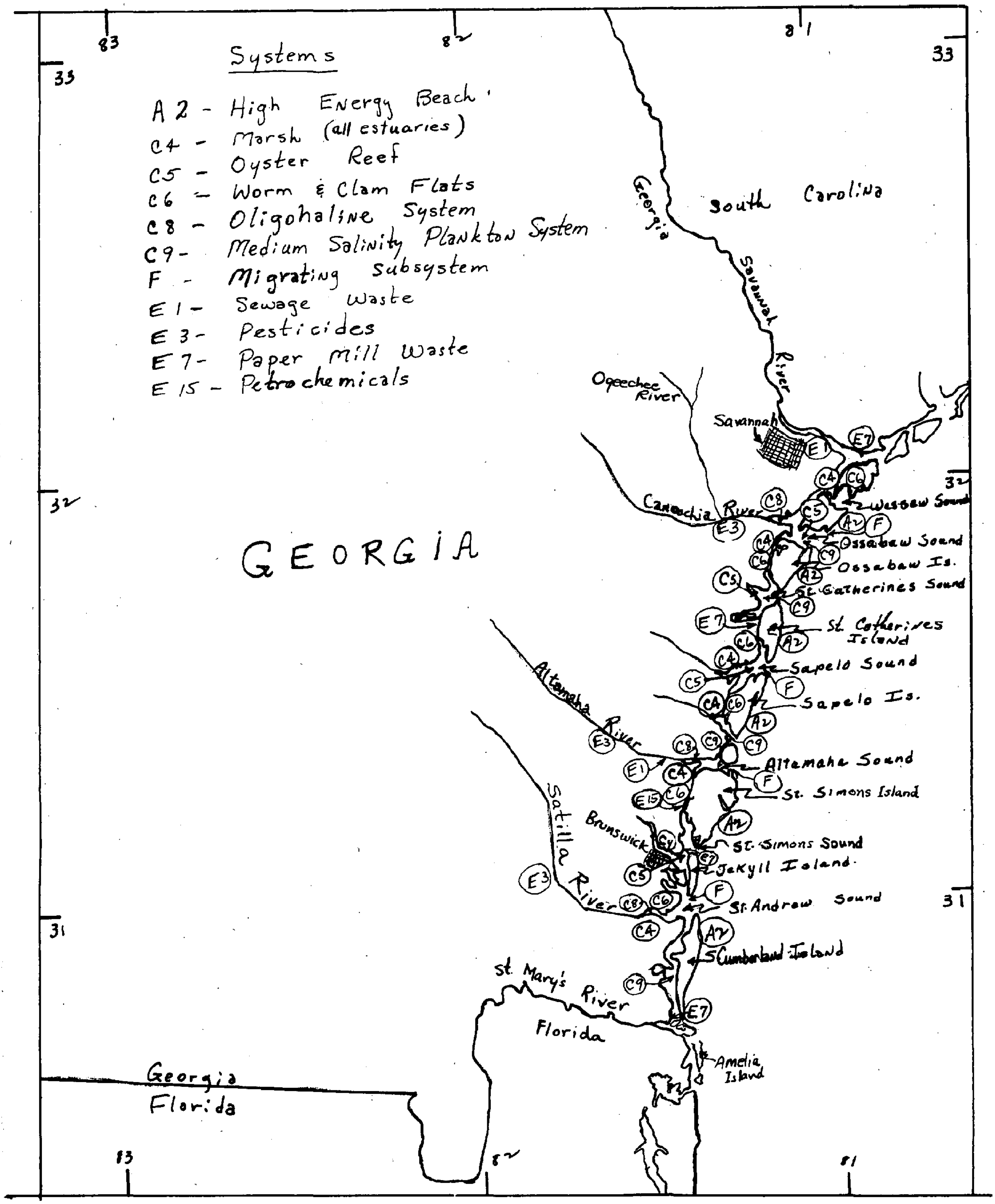

Systems
A 2 - High Energy Beach
C4 - Marsh (all estuaries)
C5 - Oyster Reef
C6 - Worm & Clam Flats
C8 - Oligohaline System
C9 - Medium Salinity Plankton System
F - Migrating subsystem
E1 - Sewage Waste
E3 - Pesticides
E7 - Paper mill Waste
E15 - Petrochemicals
83
82
81
33
32
31
GEORGIA
Georgia
South Carolina
Savannah River
Ogeechee River
Savannah
Canoochia River
Wassaw Sound
Ossabaw Sound
Ossabaw Is.
St. Catherines Sound
St. Catherines Island
Sapelo Sound
Sapelo Is.
Altamaha River
Altamaha Sound
St. Simons Island
Brunswick
St. Simons Sound
Jekyll Island
Satilla River
St. Andrew Sound
Cumberland Island
St. Mary's River
Florida
Amelia Island
Georgia
Florida

Fig. 4. Georgia

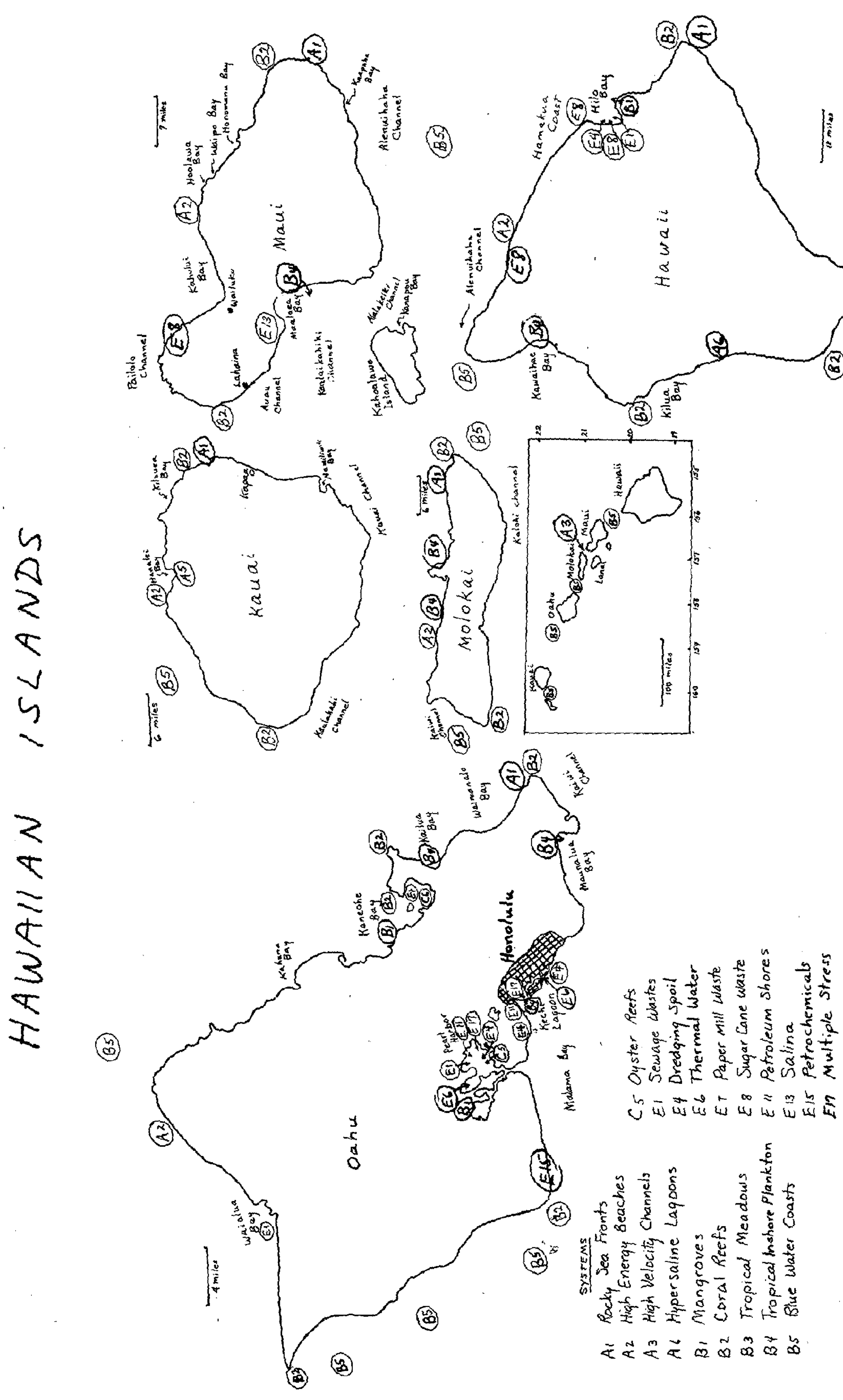

HAWAIIAN ISLANDS
Oahu
Honolulu
Kauai
Molokai
Maui
Hawaii
Kahoolawe Island
Waialua Bay
Kahana Bay
Kaneohe Bay
Kailua Bay
Waimanalo Bay
Maunalua Bay
Keehi Lagoon
Pearl Harbor
Malama Bay
Kaiwi Channel
Kauai Channel
Kaulakahi Channel
Hanalei Bay
Kilauea Bay
Kalohi Channel
Pailolo Channel
Auau Channel
Kealaikahiki Channel
Alenuihaha Channel
Kahului Bay
Maalaea Bay
Hoolawa Bay
Waipio Bay
Honomanu Bay
Kawaihae Bay
Kailua Bay
Hilo Bay
Hamakua Coast
Lahaina
Wailuku
6 miles
4 miles
7 miles
100 miles
SYSTEMS
A1 Rocky Sea Fronts
A2 High Energy Beaches
A3 High Velocity Channels
A6 Hypersaline Lagoons
B1 Mangroves
B2 Coral Reefs
B3 Tropical Meadows
B4 Tropical Inshore Plankton
B5 Blue Water Coasts
C5 Oyster Reefs
E1 Sewage Wastes
E4 Dredging Spoil
E6 Thermal Water
E7 Paper Mill Waste
E8 Sugar Cane Waste
E11 Petroleum Shores
E13 Salina
E15 Petrochemicals
E17 Multiple Stress

Fig. 5. Hawaiian Islands

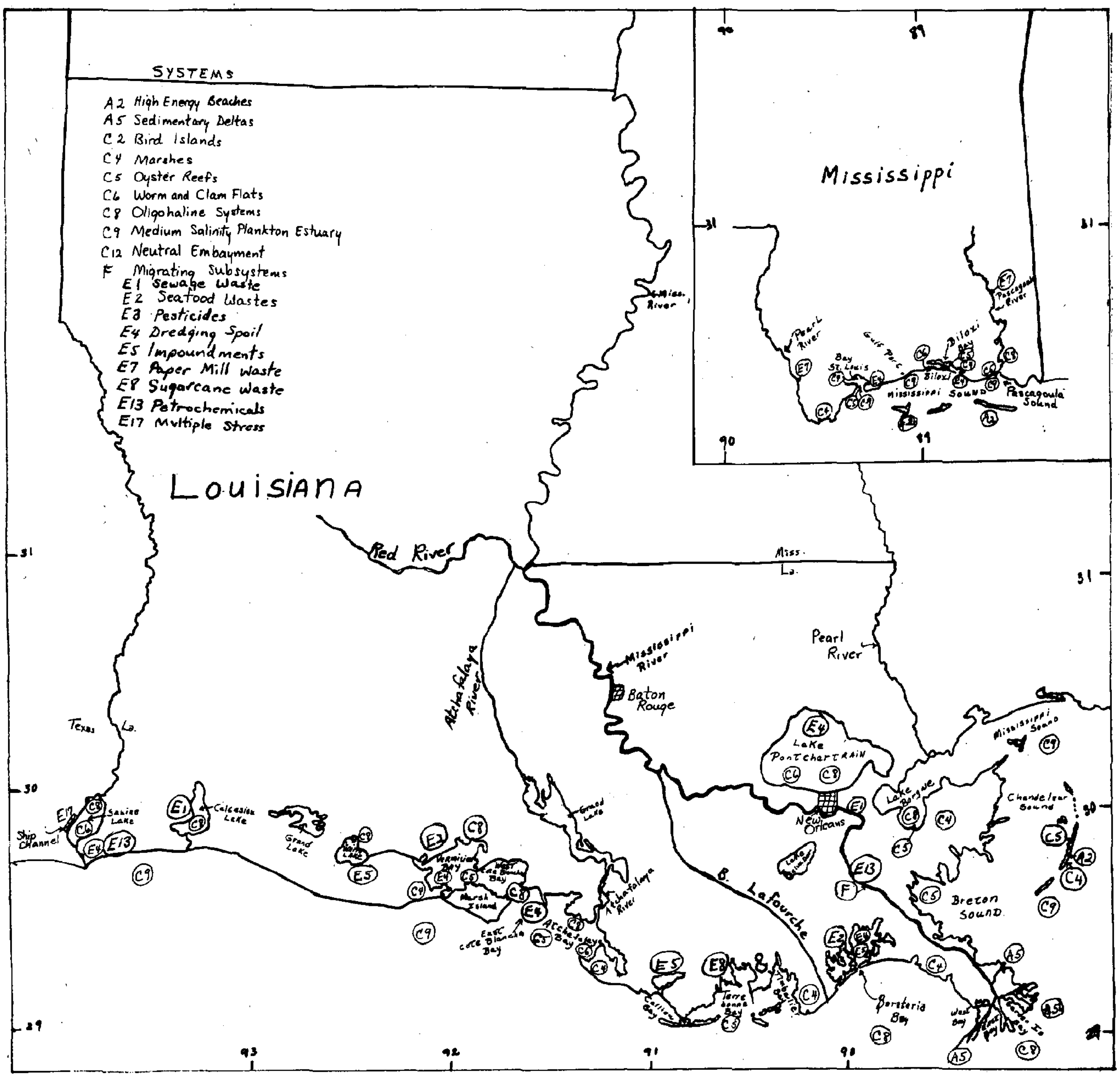

SYSTEMS
A2 High Energy Beaches
A5 Sedimentary Deltas
C2 Bird Islands
C4 Marshes
C5 Oyster Reefs
C6 Worm and Clam Flats
C8 Oligohaline Systems
C9 Medium Salinity Plankton Estuary
C12 Neutral Embayment
F Migrating Subsystems
E1 Sewage Waste
E2 Seafood Wastes
E3 Pesticides
E4 Dredging Spoil
E5 Impoundments
E7 Paper Mill Waste
E8 Sugarcane Waste
E13 Petrochemicals
E17 Multiple Stress
Louisiana
Mississippi
Red River
Miss. River
Miss.
La.
Mississippi River
Baton Rouge
Atchafalaya River
Pearl River
Texas
La.
Ship Channel
Sabine Lake
Calcasieu Lake
Grand Lake
Vermilion Bay
West Cote Blanche Bay
Marsh Island
East Cote Blanche Bay
Atchafalaya Bay
Grand Lake
Atchafalaya River
Caillou Bay
Terre bonne Bay
B. Lafourche
Lake Pontchartrain
New Orleans
Lake Borgne
Mississippi Sound
Chandeleur Sound
Breton Sound
Barataria Bay
West Bay
East Bay
Bay St. Louis
Gulf Port
Biloxi
Biloxi Bay
Pascagoula River
Mississippi Sound
Pascagoula Sound
90
89
31
30
29
93
92
91

Fig. 6. Louisiana and Mississippi

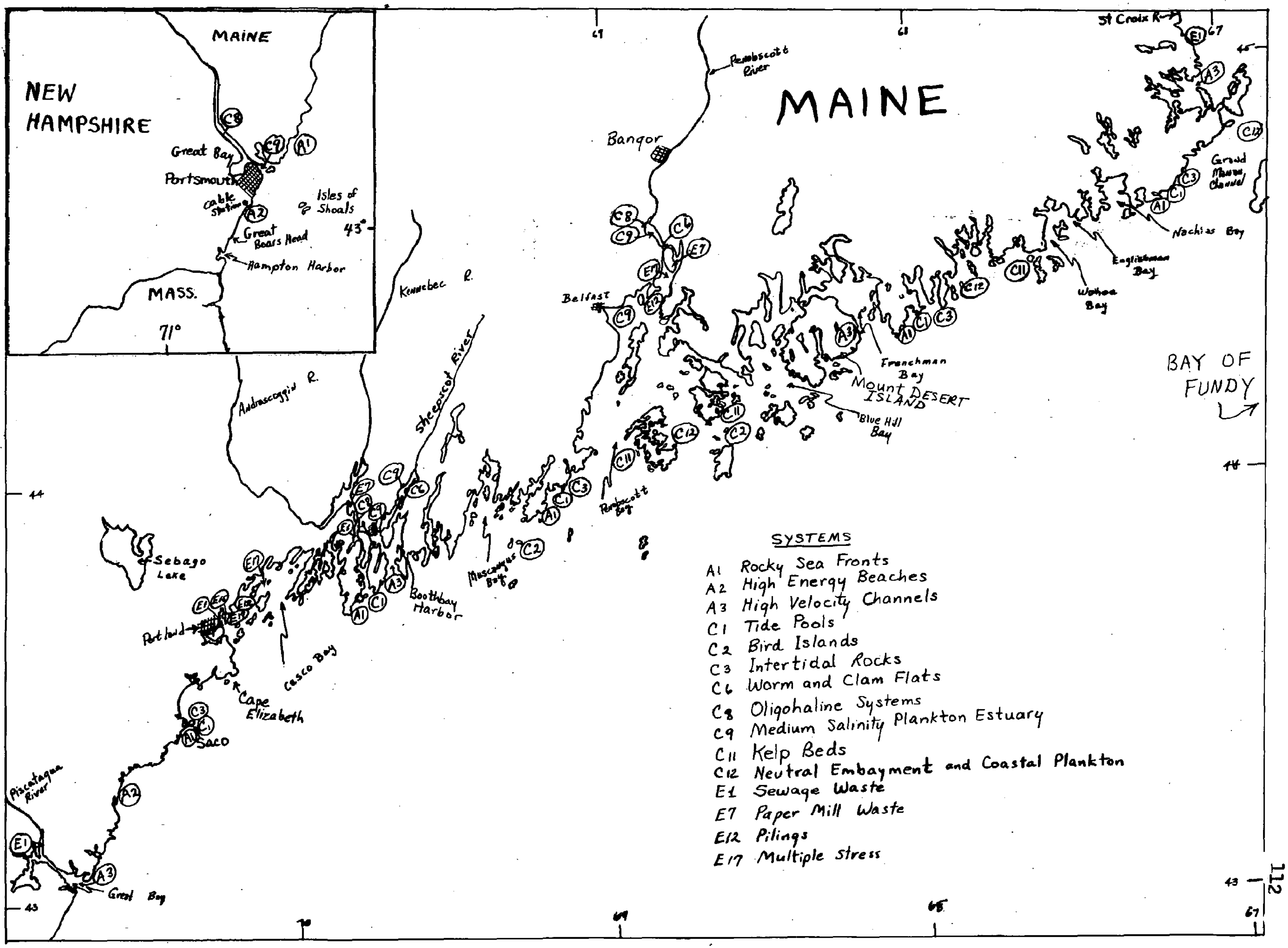

NEW HAMPSHIRE
MAINE
MASS.
C8
C9
A1
Great Bay
Portsmouth
Cable Station
A2
Isles of Shoals
43°
Great Boars Head
Hampton Harbor
71°
Kennebec R.
Androscoggin R.
Sheepscot River
Sebago Lake
Portland
E1
E12
E17
E7
Casco Bay
Cape Elizabeth
C3
C1
A1
Saco
A2
A3
Great Bay
Piscataqua River
E1
44
43
C9
C6
Boothbay Harbor
A3
C1
A1
Muscongus Bay
C2
Penobscot Bay
C11
C12
C2
Belfast
Bangor
Penobscot River
C8
C9
C6
E7
E12
MAINE
Frenchman Bay
Mount DESERT ISLAND
Blue Hill Bay
A3
C11
E12
C3
Wohoa Bay
Englishman Bay
Machias Bay
Grand Manan Channel
C12
St Croix R.
67
45
BAY OF FUNDY
44
43
SYSTEMS
A1 Rocky Sea Fronts
A2 High Energy Beaches
A3 High Velocity Channels
C1 Tide Pools
C2 Bird Islands
C3 Intertidal Rocks
C6 Worm and Clam Flats
C8 Oligohaline Systems
C9 Medium Salinity Plankton Estuary
C11 Kelp Beds
C12 Neutral Embayment and Coastal Plankton
E1 Sewage Waste
E7 Paper Mill Waste
E12 Pilings
E17 Multiple Stress

Fig. 7. Maine and New Hampshire

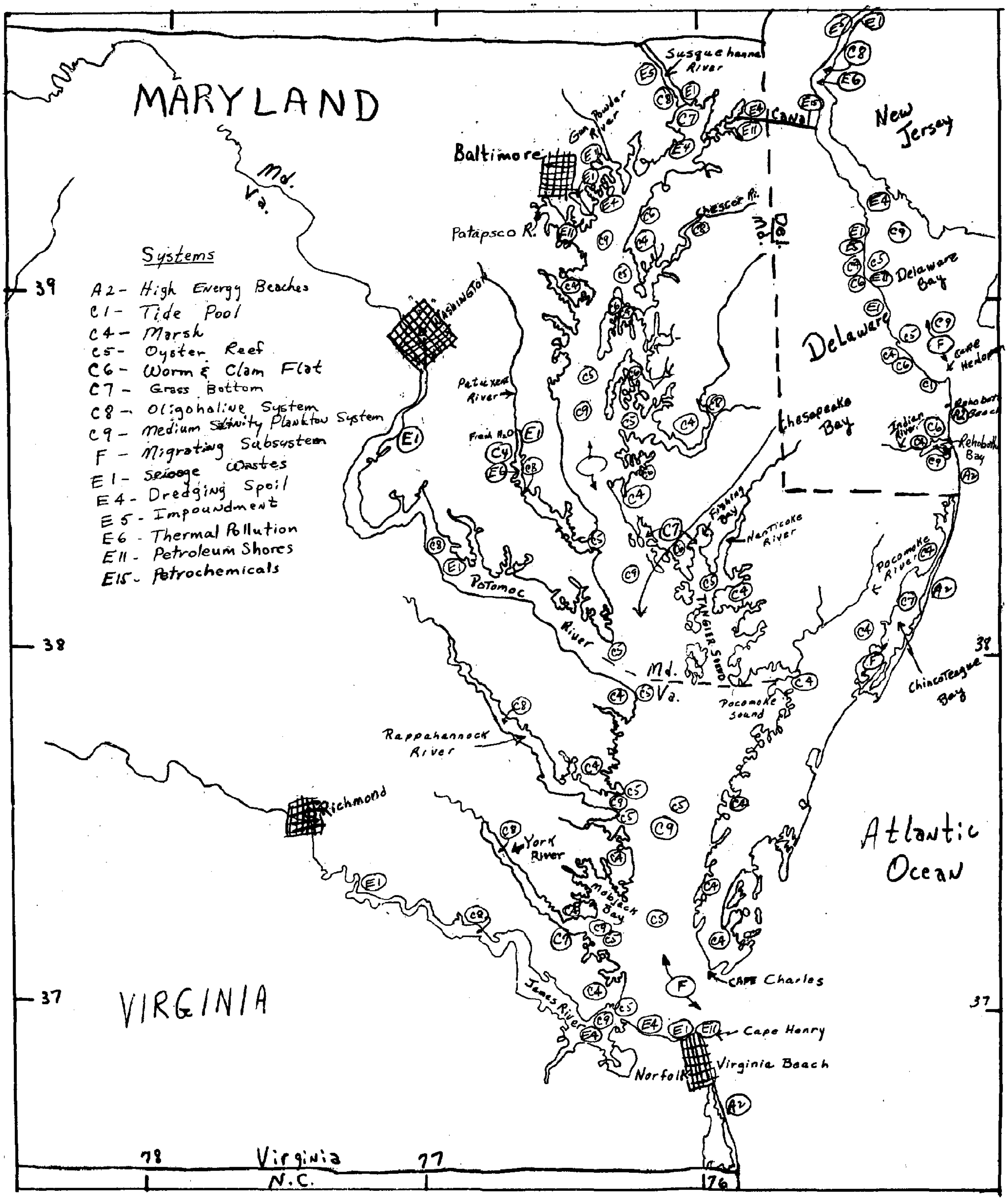

MARYLAND
Md.
Va.
Systems
A2- High Energy Beaches
C1- Tide Pool
C4- Marsh
C5- Oyster Reef
C6- Worm & Clam Flat
C7- Grass Bottom
C8- Oligohaline System
C9- Medium Salinity Plankton System
F - Migrating Subsystem
E1 - Sewage Wastes
E4 - Dredging Spoil
E5 - Impoundment
E6 - Thermal Pollution
E11 - Petroleum Shores
E15 - Petrochemicals
39
38
37
Baltimore
Patapsco R.
Washington
Susquehanna River
Gunpowder River
Canal
Chester R.
Md.
Del.
New Jersey
Delaware Bay
Delaware
Cape Henlopen
Rehoboth Beach
Indian River
Rehoboth Bay
Chesapeake Bay
Patuxent River
Fresh H2O
Fishing Bay
Nanticoke River
Tangier Sound
Pocomoke River
Chincoteague Bay
Potomac River
Md.
Va.
Pocomoke Sound
Rappahannock River
Richmond
York River
Mobjack Bay
Atlantic Ocean
Cape Charles
James River
Cape Henry
Norfolk
Virginia Beach
VIRGINIA
78
77
76
Virginia
N.C.

Fig. 8. Maryland, Delaware, and Virginia

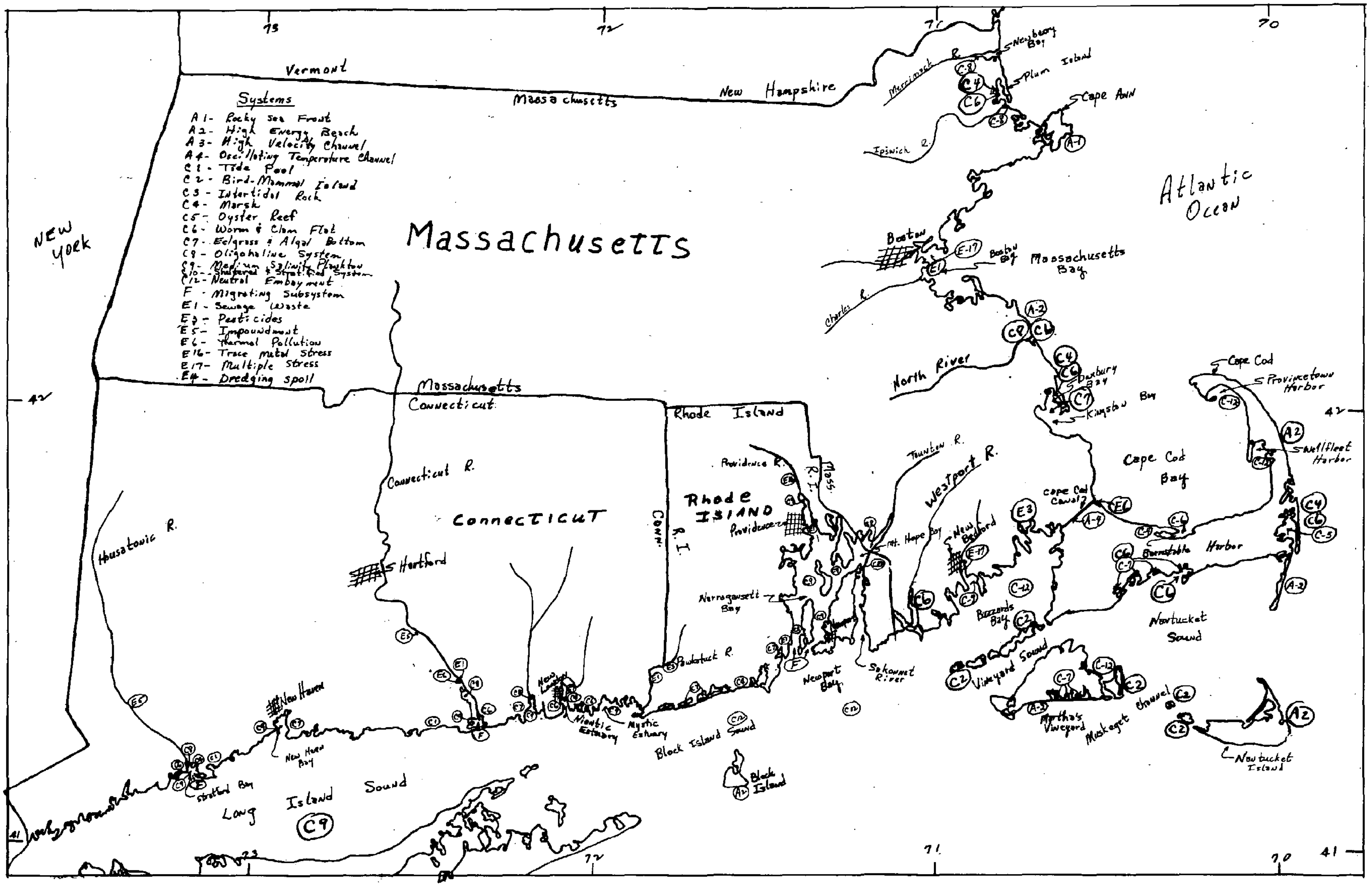

Systems
A1- Rocky Sea Front
A2- High Energy Beach
A3- High Velocity Channel
A4- Oscillating Temperature Channel
C1- Tide Pool
C2- Bird-Mammal Island
C3- Intertidal Rock
C4- Marsh
C5- Oyster Reef
C6- Worm & Clam Flat
C7- Eelgrass & Algal Bottom
C8- Oligohaline System
C9- Medium Salinity Plankton
C10- Sheltered & Stratified System
C12- Neutral Embayment
F - Migrating Subsystem
E1- Sewage Waste
E3- Pesticides
E5- Impoundment
E6- Thermal Pollution
E16- Trace metal Stress
E17- Multiple Stress
E4- Dredging spoil
73
72
71
70
42
41
New York
Vermont
New Hampshire
Massachusetts
Massachusetts
Connecticut
Rhode Island
Mass.
R.I.
Conn.
Rhode Island
Connecticut
Atlantic Ocean
Newbury Bay
Plum Island
Cape Ann
Merrimack R.
Ipswich R.
Boston
Boston Bay
Massachusetts Bay
Charles R.
North River
Duxbury Bay
Kingston Bay
Cape Cod
Provincetown Harbor
Wellfleet Harbor
Cape Cod Bay
Cape Cod Canal
Barnstable Harbor
Nantucket Sound
Taunton R.
Westport R.
Providence R.
Providence
Mt. Hope Bay
New Bedford
Buzzards Bay
Narragansett Bay
Newport Bay
Sakonnet River
Pawcatuck R.
Vineyard Sound
Martha's Vineyard
Muskeget Channel
Nantucket Island
Block Island
Block Island Sound
Mystic Estuary
Niantic Estuary
New London
Connecticut R.
Hartford
Housatonic R.
New Haven
New Haven Bay
Stratford Bay
Long Island Sound

Fig. 9. Massachusetts, Rhode Island, Connecticut

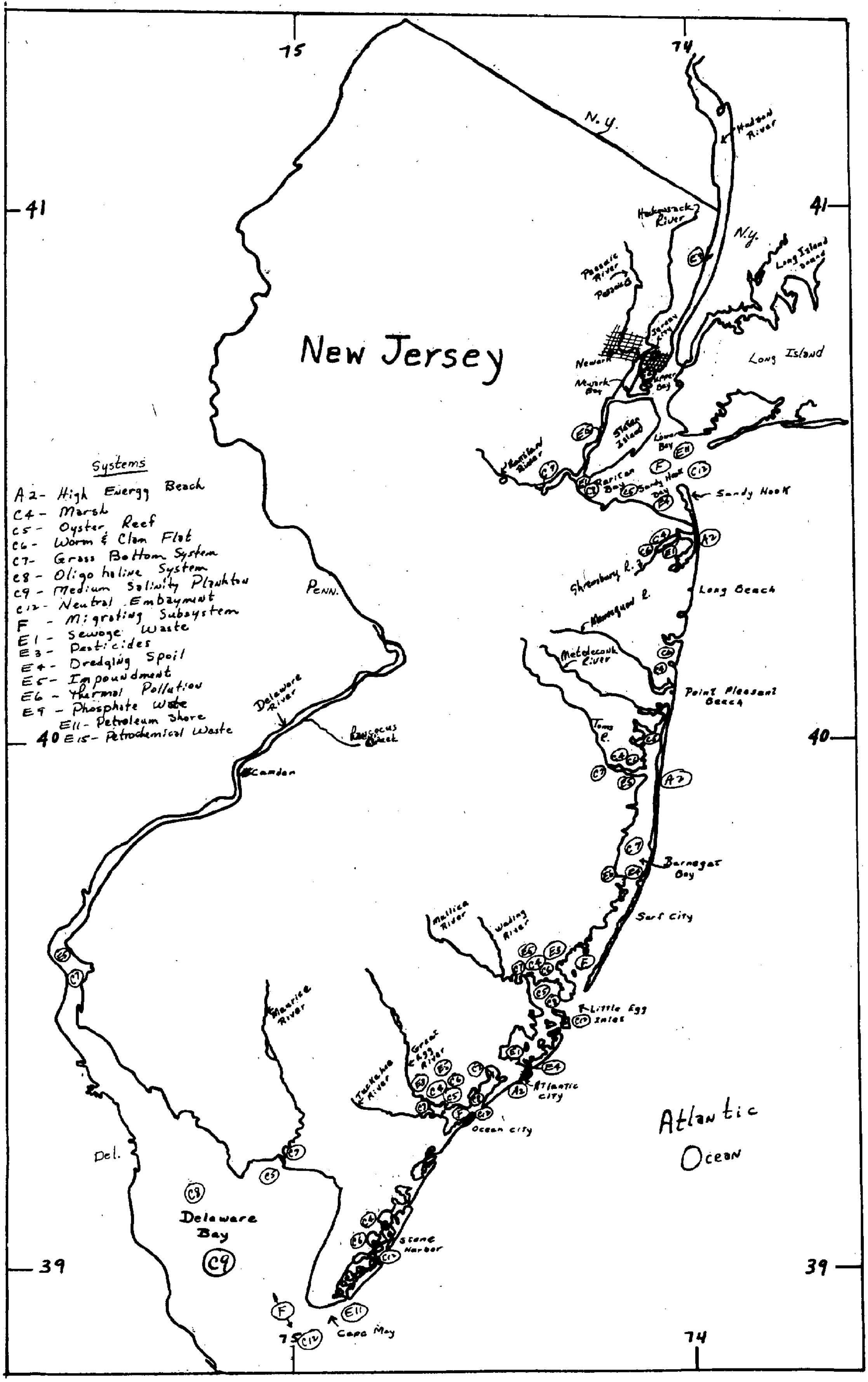

75
74
41
40
39
N.Y.
Hudson River
Hackensack River
N.Y.
Long Island Sound
Passaic River
Passaic
Jersey City
Newark
Newark Bay
Upper Bay
Long Island
New Jersey
Staten Island
Lower Bay
Raritan River
Raritan Bay
Sandy Hook Bay
Sandy Hook
Shrewsbury R.
Long Beach
Manasquan R.
Metedeconk River
Point Pleasant Beach
Toms R.
Barnegat Bay
Surf City
Mullica River
Wading River
Little Egg Inlet
Maurice River
Great Egg River
Tuckahoe River
Atlantic City
Ocean city
Atlantic Ocean
Stone Harbor
Cape May
Del.
Delaware Bay
Penn.
Delaware River
Rancocus Creek
Camden
Systems
A2 - High Energy Beach
C4 - Marsh
C5 - Oyster Reef
C6 - Worm & Clam Flat
C7 - Grass Bottom System
C8 - Oligo haline System
C9 - Medium Salinity Plankton
C12 - Neutral Embayment
F - Migrating Subsystem
E1 - Sewage Waste
E3 - Pesticides
E4 - Dredging Spoil
E5 - Impoundment
E6 - Thermal Pollution
E9 - Phosphate Waste
E11 - Petroleum Shore
E15 - Petrochemical Waste

Fig. 10. New Jersey

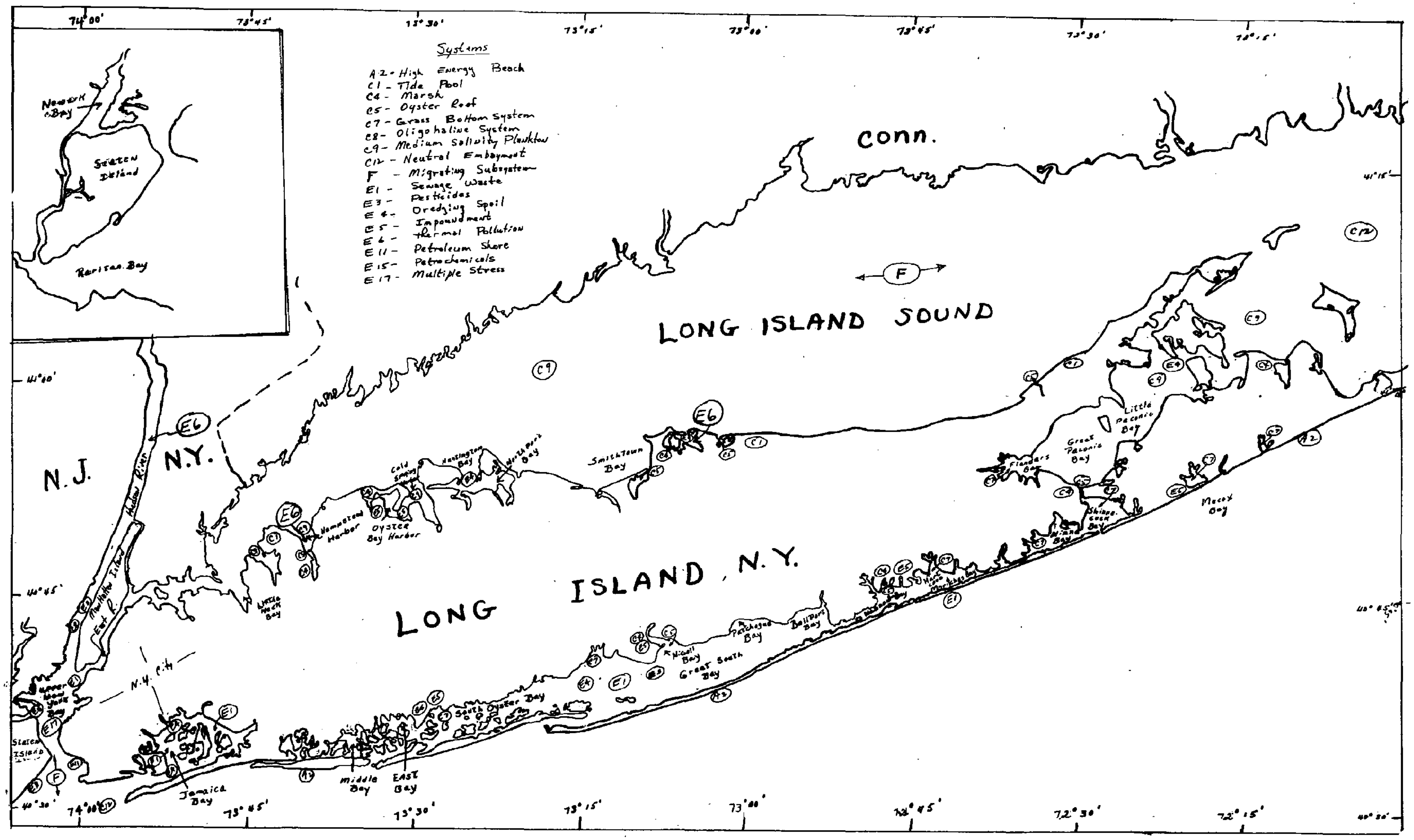

Systems
A2 - High Energy Beach
C1 - Tide Pool
C4 - Marsh
C5 - Oyster Reef
C7 - Grass Bottom System
C8 - Oligohaline System
C9 - Medium Salinity Plankton
C12 - Neutral Embayment
F - Migrating Subsystem
E1 - Sewage Waste
E3 - Pesticides
E4 - Dredging Spoil
E5 - Impoundment
E6 - thermal Pollution
E11 - Petroleum Shore
E15 - Petrochemicals
E17 - Multiple Stress
CONN.
LONG ISLAND SOUND
LONG ISLAND, N.Y.
N.J.
N.Y.
Newark Bay
Staten Island
Raritan Bay
Hudson River
Manhattan Island
East R.
N.Y. City
Upper New York Bay
Jamaica Bay
Middle Bay
East Bay
South Oyster Bay
Great South Bay
Nicoll Bay
Patchogue Bay
Bellport Bay
Moriches Bay
Shinnecock Bay
Mecox Bay
Flanders Bay
Great Peconic Bay
Little Peconic Bay
Little Neck Bay
Hempstead Harbor
Oyster Bay Harbor
Cold Spring Harbor
Huntington Bay
Northport Bay
Smithtown Bay
74° 00'
73° 45'
73° 30'
73° 15'
73° 00'
72° 45'
72° 30'
72° 15'
41° 15'
41° 00'
40° 45'
40° 30'

Fig. 11. Long Island, N.Y.

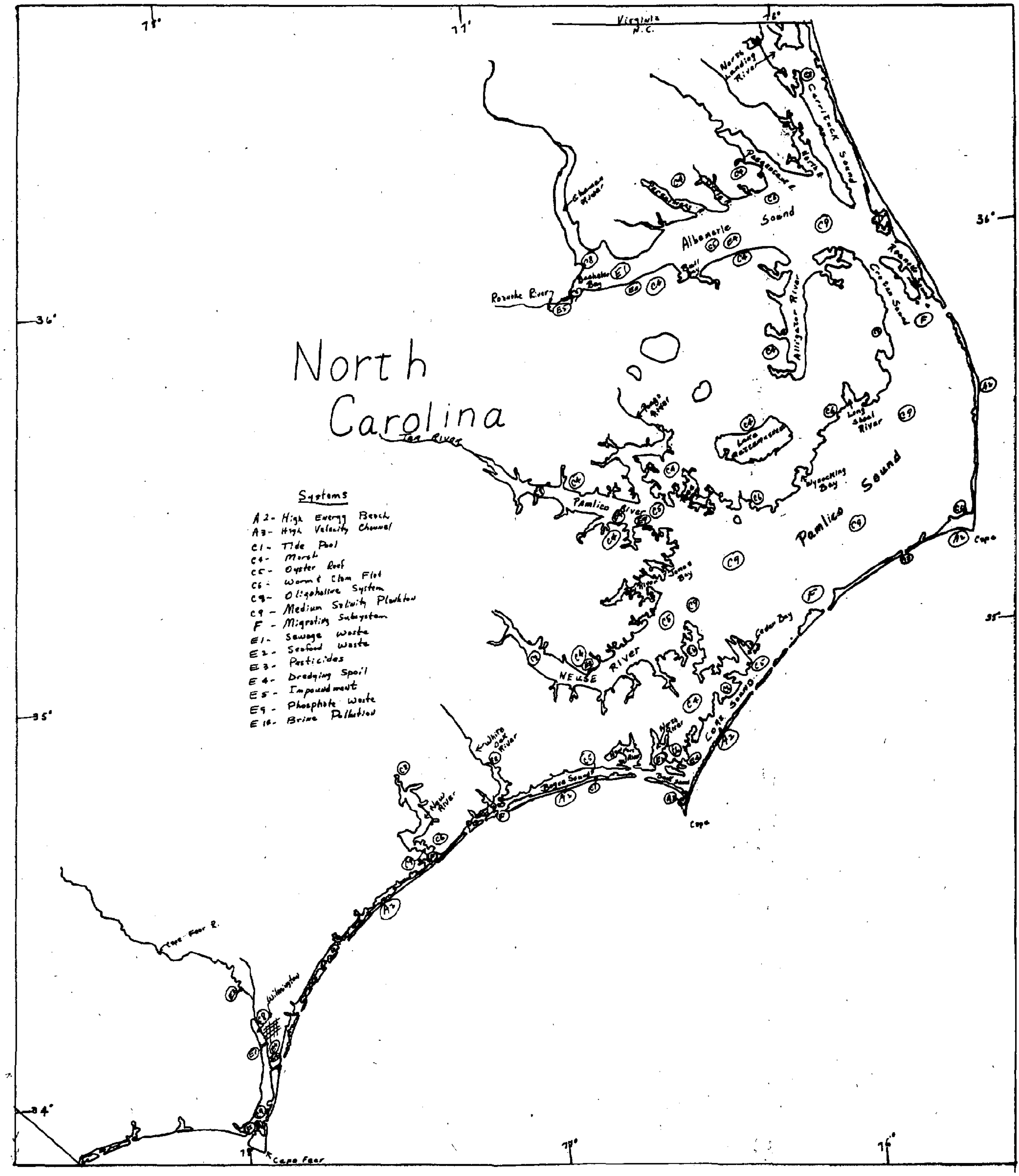

Virginia
N.C.
78°
77°
76°
36°
35°
34°
North Carolina
North Landing River
Currituck Sound
Pasquotank R.
Perquimans
Chowan River
Albemarle Sound
Roanoke River
Bull Bay
Alligator River
Croatan Sound
Roanoke Island
Lake Mattamuskeet
Long Shoal River
Wysocking Bay
Pamlico Sound
Tar River
Pungo River
Pamlico River
Bay River
Jones Bay
Neuse River
Cedar Bay
Core Sound
North River
Back Sound
Bogue Sound
White Oak River
New River
Cape Fear R.
Wilmington
Cape
Cape Fear
Systems
A2 - High Energy Beach
A3 - High Velocity Channel
C1 - Tide Pool
C4 - Marsh
C5 - Oyster Reef
C6 - Worm & Clam Flat
C8 - Oligohaline System
C9 - Medium Salinity Plankton
F - Migrating Subsystem
E1 - Sewage Waste
E2 - Seafood Waste
E3 - Pesticides
E4 - Dredging Spoil
E5 - Impoundment
E9 - Phosphate Waste
E10 - Brine Pollution

Fig. 12. North Carolina

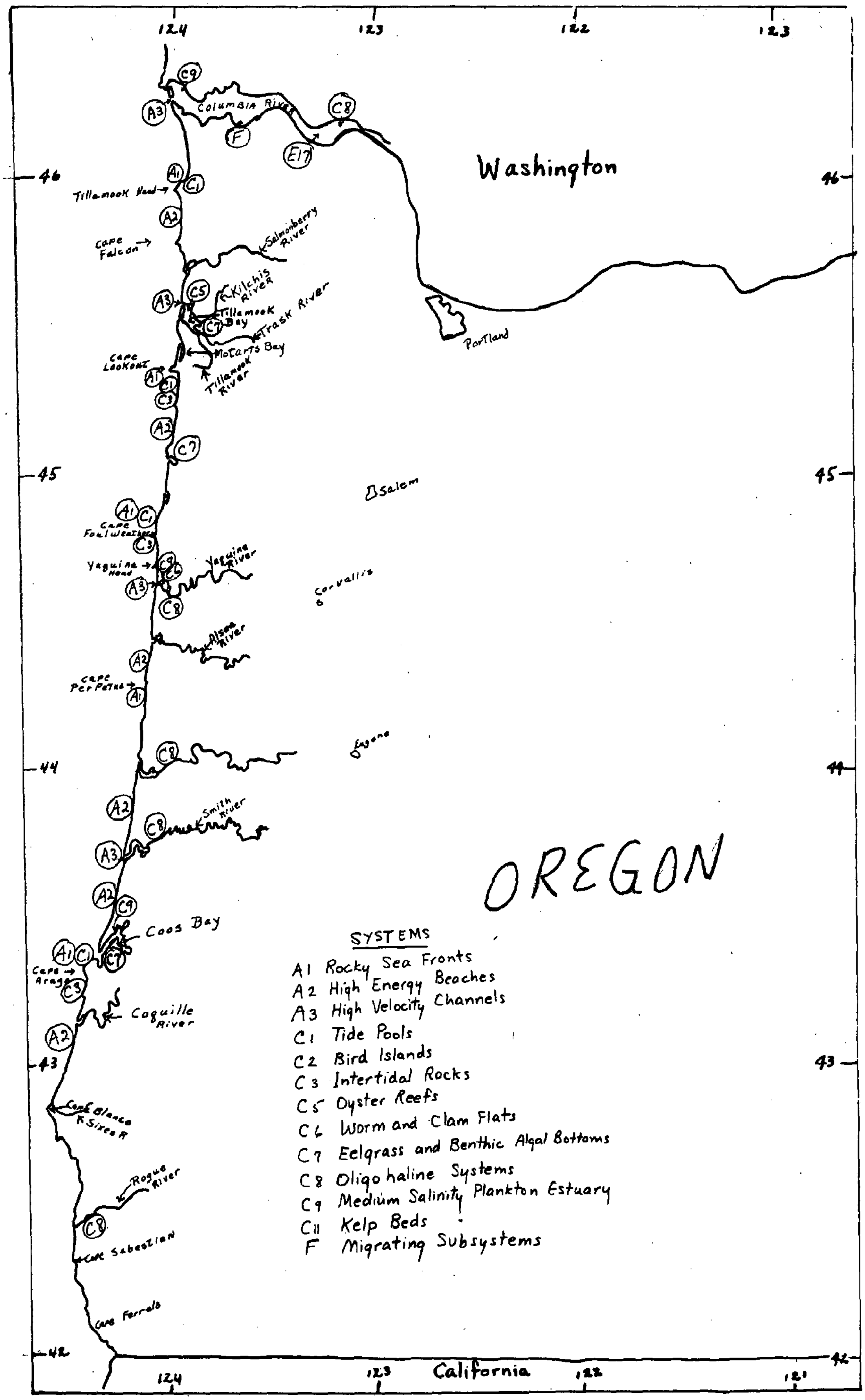

124
123
122
123
46
45
44
43
42
Washington
Columbia River
C9
A3
F
C8
E17
A1
C1
Tillamook Head
A2
Cape Falcon
Salmonberry River
C5
A3
Kilchis River
Tillamook Bay
C7
Trask River
Motarts Bay
Cape Lookout
Tillamook River
A1
C1
C3
A2
C7
Portland
Salem
A1
C1
Cape Foulweather
C3
Yaquina Head
C9
C6
Yaquina River
A3
C8
Corvallis
Alsea River
A2
Cape Perpetua
A1
C8
Eugene
A2
C8
Smith River
A3
A2
C9
Coos Bay
A1
C1
C7
Cape Arago
C3
Coquille River
A2
Cape Blanco
Sixes R
Rogue River
C8
Cape Sebastian
Cape Ferrelo
OREGON
SYSTEMS
A1 Rocky Sea Fronts
A2 High Energy Beaches
A3 High Velocity Channels
C1 Tide Pools
C2 Bird Islands
C3 Intertidal Rocks
C5 Oyster Reefs
C6 Worm and Clam Flats
C7 Eelgrass and Benthic Algal Bottoms
C8 Oligohaline Systems
C9 Medium Salinity Plankton Estuary
C11 Kelp Beds
F Migrating Subsystems
California
124
123
122
121

Fig. 13. Oregon

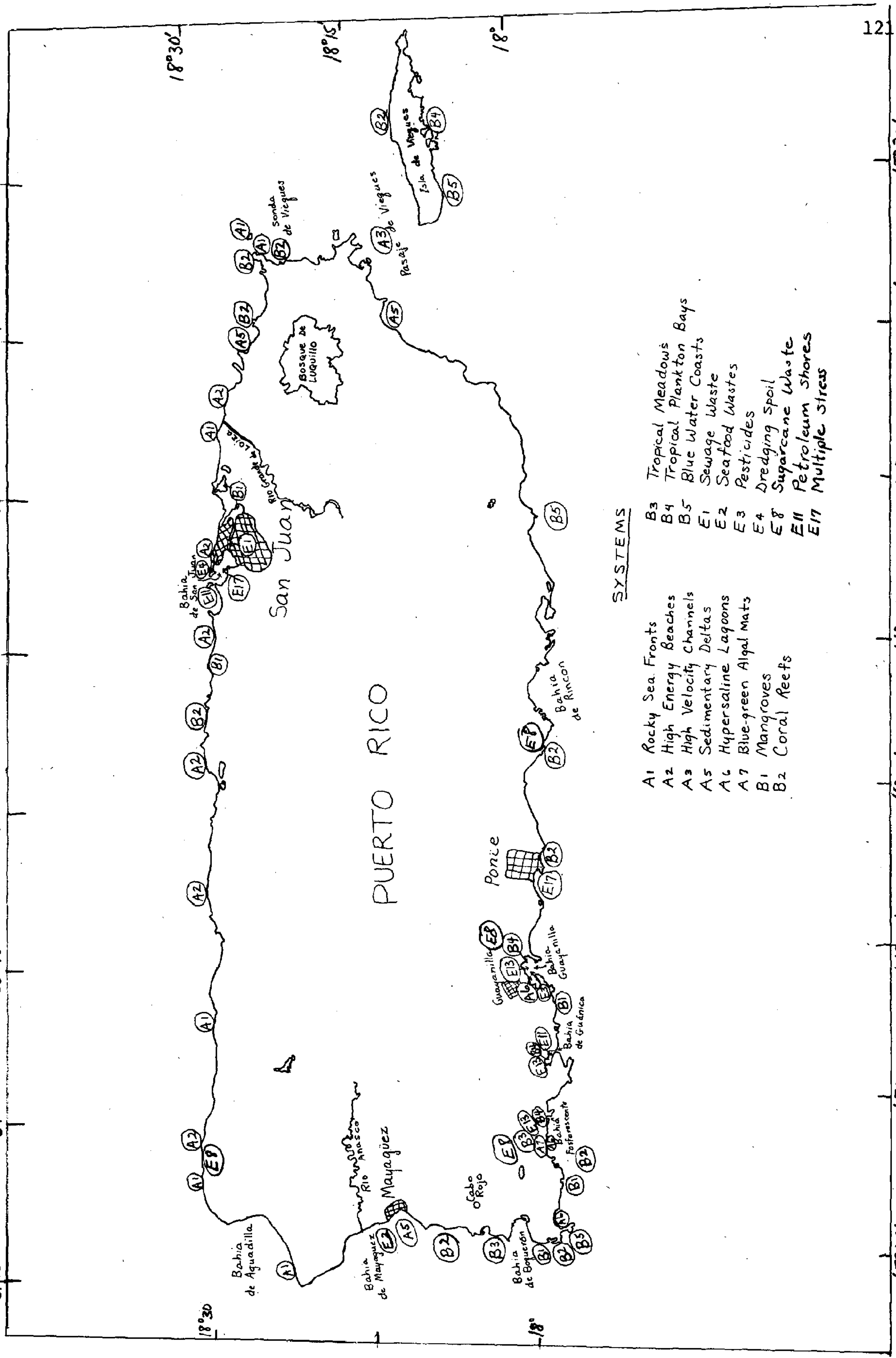

PUERTO RICO
San Juan
Bahia de San Juan
Rio Grande de Loiza
Bosque de Luquillo
Sonda de Vieques
Pasaje de Vieques
Isla de Vieques
Bahia de Rincon
Ponce
Guayanilla
Bahia Guayanilla
Bahia de Guánica
Bahia Fosforescente
Cabo Rojo
Bahia de Boquerón
Mayagüez
Bahia de Mayagüez
Rio Añasco
Bahia de Aguadilla
18°30'
18°15'
18°
65°30'
65°45'
66°
66°15'
66°30'
66°45'
67°
67°15'
SYSTEMS
A1 Rocky Sea Fronts
A2 High Energy Beaches
A3 High Velocity Channels
A5 Sedimentary Deltas
A6 Hypersaline Lagoons
A7 Blue-green Algal Mats
B1 Mangroves
B2 Coral Reefs
B3 Tropical Meadows
B4 Tropical Plankton Bays
B5 Blue Water Coasts
E1 Sewage Waste
E2 Seafood Wastes
E3 Pesticides
E4 Dredging Spoil
E8 Sugarcane Waste
E11 Petroleum Shores
E17 Multiple Stress

Fig. 14. Puerto Rico

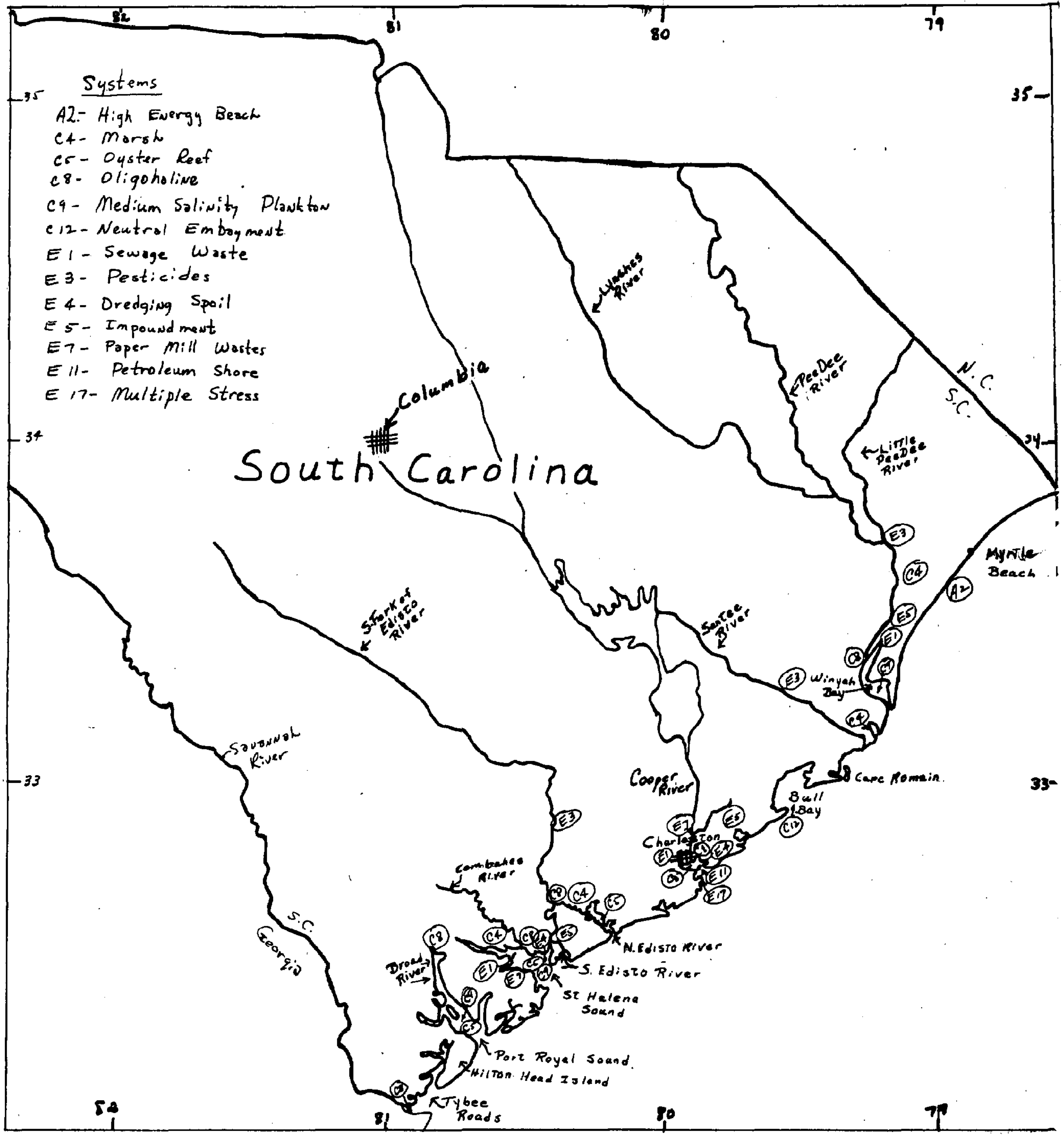

Systems
A2- High Energy Beach
C4- Marsh
C5- Oyster Reef
C8- Oligohaline
C9- Medium Salinity Plankton
C12- Neutral Embayment
E1 - Sewage Waste
E3 - Pesticides
E4 - Dredging Spoil
E5 - Impoundment
E7 - Paper Mill Wastes
E11 - Petroleum Shore
E17 - Multiple Stress
82
81
80
79
35
34
33
South Carolina
Columbia
Lynches River
PeeDee River
Little PeeDee River
N.C.
S.C.
Myrtle Beach
A2
E3
C4
E5
E1
C8
C9
Winyah Bay
Santee River
S. Fork of Edisto River
Savannah River
S.C.
Georgia
Cooper River
Cape Romain
Bull Bay
C12
Charleston
E7
E1
E4
E11
E17
Combahee River
N. Edisto River
S. Edisto River
St Helena Sound
Broad River
Port Royal Sound
Hilton Head Island
Tybee Roads

Fig. 15. South Carolina

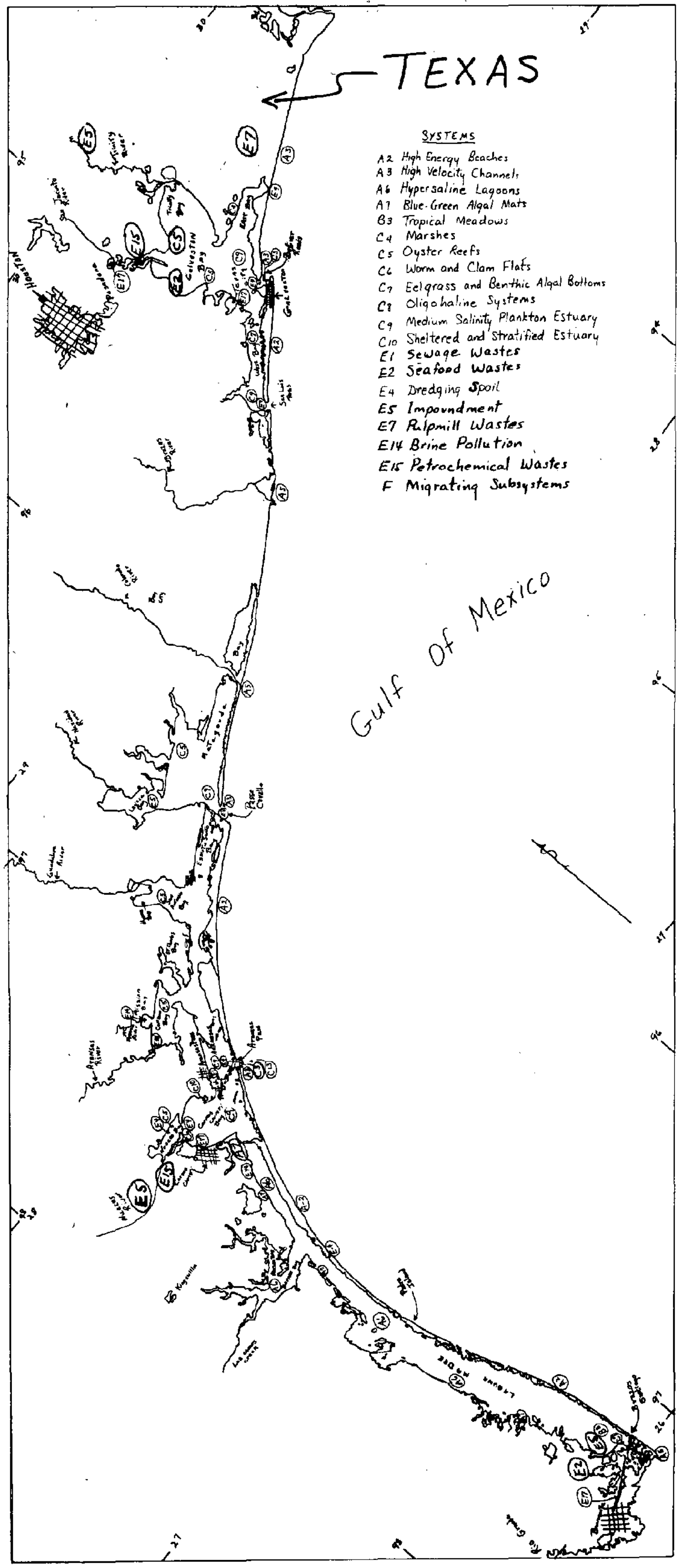

TEXAS
SYSTEMS
A2 High Energy Beaches
A3 High Velocity Channels
A6 Hypersaline Lagoons
A7 Blue-Green Algal Mats
B3 Tropical Meadows
C4 Marshes
C5 Oyster Reefs
C6 Worm and Clam Flats
C7 Eelgrass and Benthic Algal Bottoms
C8 Oligohaline Systems
C9 Medium Salinity Plankton Estuary
C10 Sheltered and Stratified Estuary
E1 Sewage Wastes
E2 Seafood Wastes
E4 Dredging Spoil
E5 Impoundment
E7 Pulpmill Wastes
E14 Brine Pollution
E15 Petrochemical Wastes
F Migrating Subsystems
Gulf Of Mexico
Houston
Galveston Bay
Galveston
E5
E7
E15
E17
E2

Fig. 16. Texas

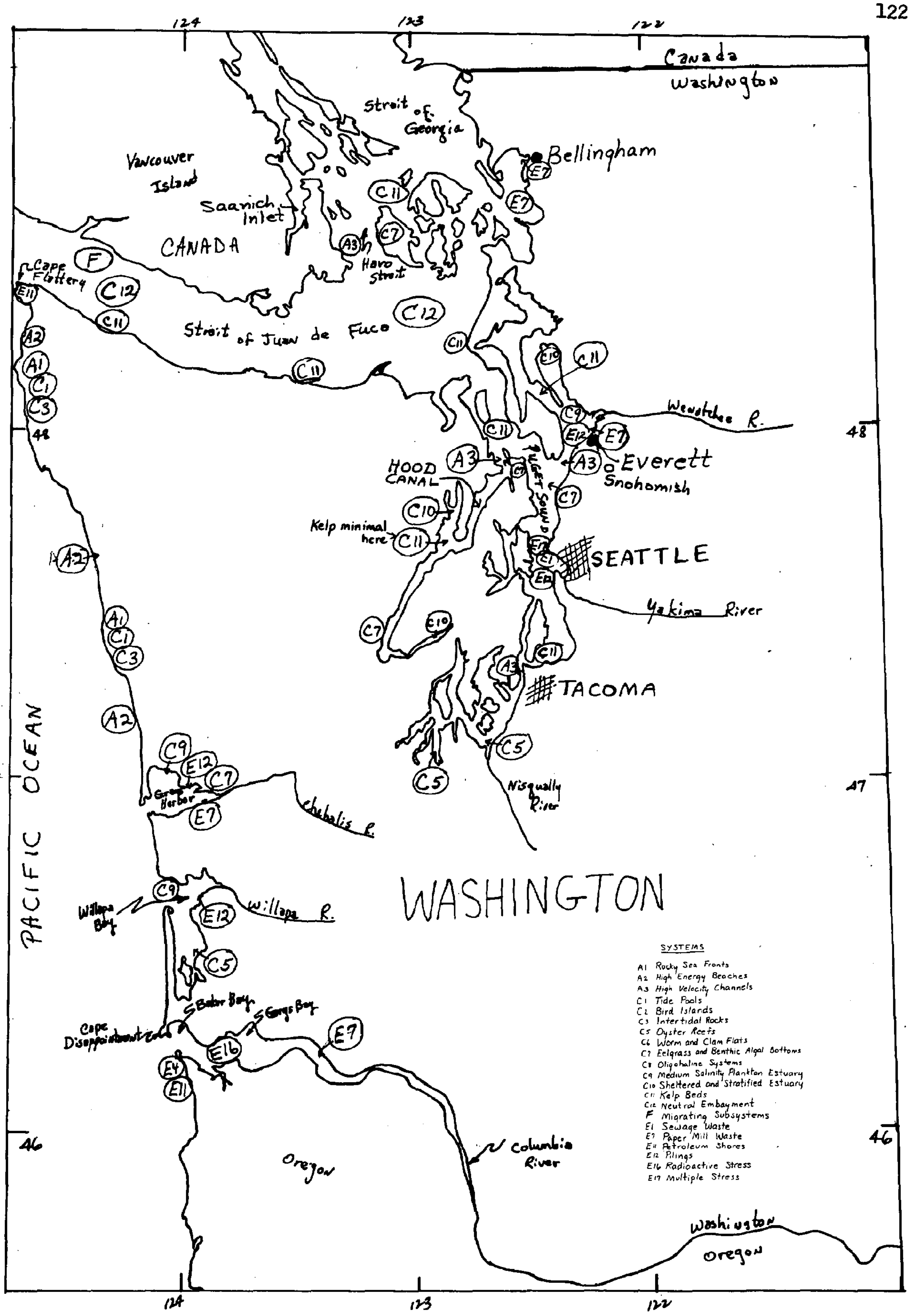
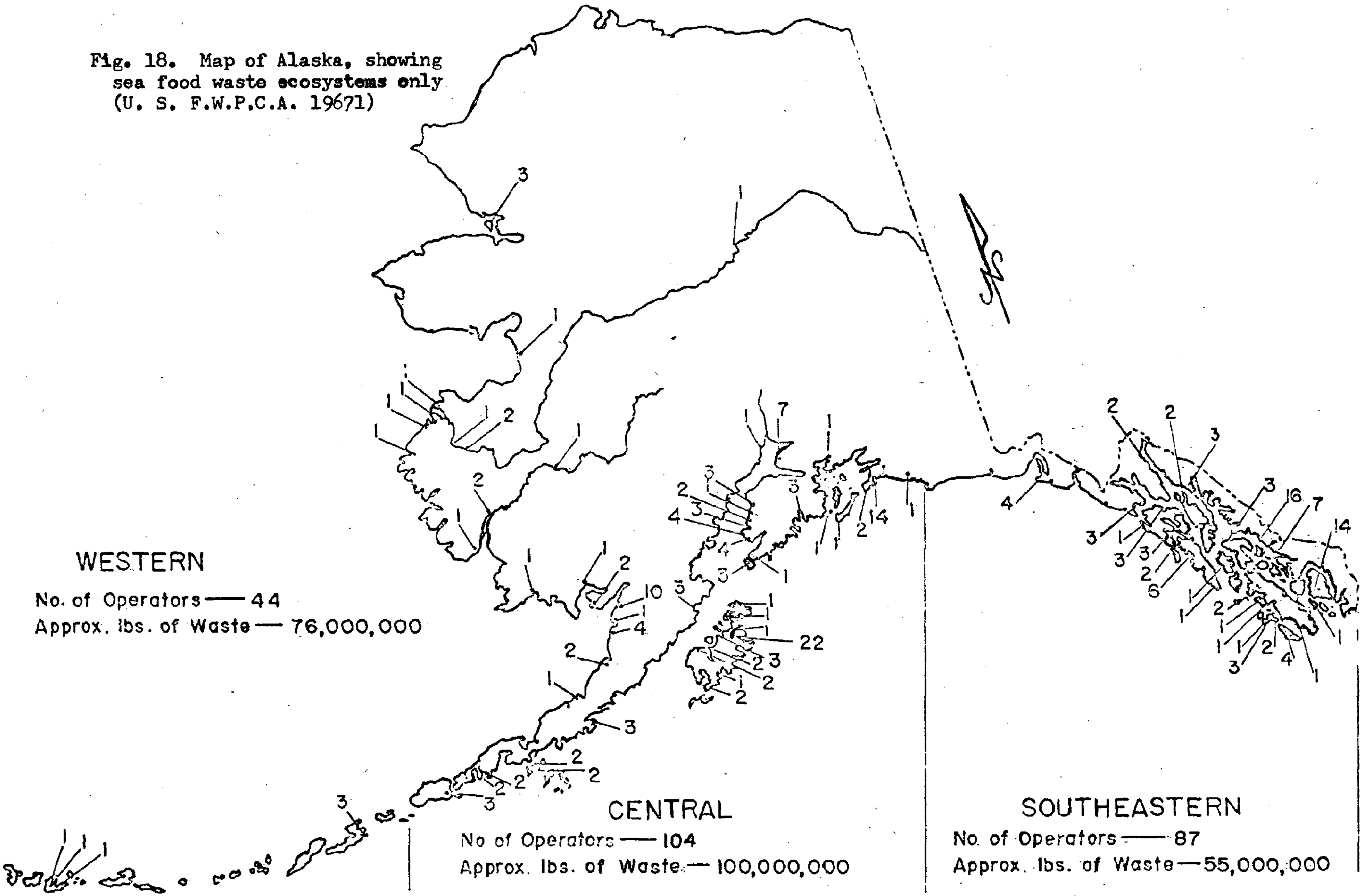

124
123
122
Canada
Washington
Strait of Georgia
Bellingham
Vancouver Island
Saanich Inlet
CANADA
Haro Strait
Cape Flattery
F
Strait of Juan de Fuca
Wenatchee R.
48
HOOD CANAL
Puget Sound
Everett
Snohomish
Kelp minimal here
SEATTLE
Yakima River
TACOMA
Nisqually River
PACIFIC OCEAN
47
Grays Harbor
Chehalis R.
WASHINGTON
Willapa Bay
Willapa R.
Baker Bay
Grays Bay
Cape Disappointment
Columbia River
Oregon
46
Washington
Oregon
SYSTEMS
A1 Rocky Sea Fronts
A2 High Energy Beaches
A3 High Velocity Channels
C1 Tide Pools
C2 Bird Islands
C3 Intertidal Rocks
C5 Oyster Reefs
C6 Worm and Clam Flats
C7 Eelgrass and Benthic Algal Bottoms
C8 Oligohaline Systems
C9 Medium Salinity Plankton Estuary
C10 Sheltered and Stratified Estuary
C11 Kelp Beds
C12 Neutral Embayment
F Migrating Subsystems
E1 Sewage Waste
E7 Paper Mill Waste
E11 Petroleum Shores
E12 Pilings
E16 Radioactive Stress
E17 Multiple Stress

Fig. 17. Washington

Fig. 18. Map of Alaska, showing sea food waste ecosystems only (U. S. F.W.P.C.A. 19671)


WESTERN
No. of Operators — 44
Approx. lbs. of Waste — 76,000,000
CENTRAL
No of Operators — 104
Approx. lbs. of Waste — 100,000,000
SOUTHEASTERN
No. of Operators — 87
Approx. lbs. of Waste — 55,000,000

Part III-B

COASTAL ECOSYSTEMS OF ALASKA

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INTRODUCTION

Alaska lives on its coast, a coast that extends from the rain forests of Southeast Alaska to the arctic tundra. This is indeed a diverse and complex system. The gradation from temperate to arctic includes all types of coastal systems found in the lower states with the exception of the tropical systems and the systems stressed by complex pollution effluents.

Alaska has only about 300,000 people. This small population, although concentrated on the coast, has a very limited influence on the natural systems of the 47,000 miles of coastline. Nonetheless, today Alaska is experiencing rapid economic growth which is larely a result of development of the natural resources of the coast. In the last year a very large oil deposit was revealed on the arctic slope near Prudhoe Bay and this once remote coast now has more flights daily than most cities in the state; speculation exists that the development of the wealth of the arctic slope will utilize icebreaking super-tankers. Regardless of the type of development that occurs on the arctic coast, this remote area will change rapidly and much more knowledge of the coastal systems will be needed than presently exists.

The arctic coast systems of the United States are unique to Alaska. This report on the coastal systems of Alaska concentrates on the systems found only in Alaska. In addition to the arctic coast (ice stressed coast), these include sea ice and under ice plankton (systems associated with the ice-covered open sea), glacial fiords (systems associated with fiords that have icebergs), and turbid outwash fiords (systems associated with fiords receiving turbid outflow from glaciers).

This report is the result of the cooperative efforts of many people in the Institute of Marine Science, University of Alaska. The advice, criticisms, and discussions of Dr. Donald W. Hood are most gratefully appreciated. The sections on fiords were principally the results of the efforts of Dr. David Burrell and Dr. Brian Matthews. The other sections were written by Dr. Peter McRoy, Dr. John Goering, and Dr. Mary Belle Allen with contributions from Mr. John Kelley, Dr. F. F. Wright, and Dr. C. M. Hoskin. We are grateful for the technical assistance of Mrs. Laura McManus and Mrs. Rose Marie Nauman.

TYPES OF COASTAL ECOSYSTEMS IN ALASKA

The complex coast of Alaska covers a broad geographical range in latitude and longitude and includes ecosystems that grade from temperate into extreme arctic. Most systems are natural. The problems of emerging new systems associated with man are limited to the few major population centers of the coast. The geographical distribution of the systems in Alaska follows (Fig. 1, Table 1). The diversity of the Alaska coast is reflected in this list. It includes every type found in the lower states with the exception of the tropical systems and a few of the more destructive pollution systems. As a further index of the diversity of the Alaskan coast we have calculated the miles of tidal shoreline in each region. The general coastline of Alaska is 6,640 miles long, which is 54% of the total (12,383 miles) general coastline of the United States (Pederson, 1965). The tidal shoreline, which includes islands, inlets, and all shoreline to the head of tidewater, is much longer and reflects the intricacy of coastal Alaska. This distance is estimated to be 47,300 miles in Alaska and 88,633 miles in the United States. This tidal shoreline in Alaska is greatest in the Southeast region (63%), where the coast is a labyrinth of fiords, islands, bays, and rocks, and is minimal in the Arctic (2%), where the coast is a series of lagoons and barrier beaches.

Another indication of the dominance of Alaska is provided by the comparison of the areas of the continental shelves. There are three continental shelves adjacent to Alaska: the Gulf of Alaska, the Bering Sea, and the Chukchi and Beaufort (Arctic) Seas. These have areas in square miles of 140,000, 320,000, and 370,000, respectively, for a total of 830,000. The total continental shelf area for the United States is 1,120,000 square miles. The continental shelf of Alaska, then, is 74% of the total shelf of the United States.

NATURAL ARCTIC AND SUBARCTIC ECOSYSTEMS WITH ICE STRESS

The ice stressed coastal systems of the United States are unique to Alaska. There are four of these systems: glacial fiords, turbid outwash fiords, sea ice and under ice plankton, and ice stress coasts. The first two occur in Southeast and Southcentral Alaska and the last two are Arctic (Fig. 1; Table 1).

RESEARCH NEEDS

No other state has coastal systems which are not already influenced to some extent by man. Alaska is unique in this respect and perhaps the most urgently needed study involves collection of background data pertinent to understanding the natural dynamics of Alaskan coastal systems. Probably some of the systems thought to be natural have already been stressed by man's activity (e.g. global distribution of pesticides, etc.).

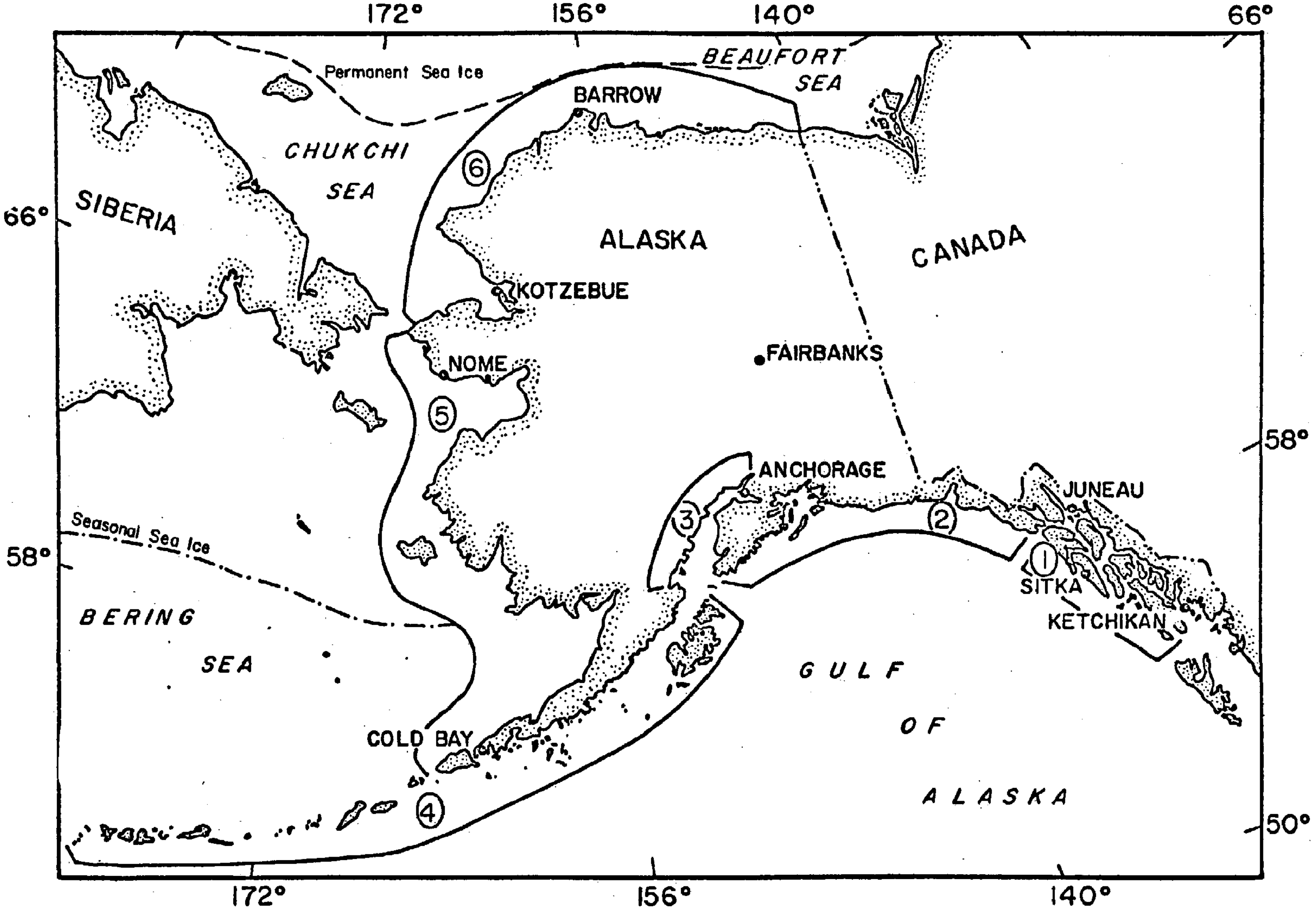

172°
156°
140°
66°
Permanent Sea Ice
BEAUFORT
SEA
BARROW
CHUKCHI
SEA
⑥
66°
SIBERIA
ALASKA
CANADA
KOTZEBUE
FAIRBANKS
NOME
⑤
58°
ANCHORAGE
JUNEAU
Seasonal Sea Ice
③
②
58°
①
SITKA
KETCHIKAN
BERING
SEA
GULF
OF
ALASKA
COLD BAY
④
50°
172°
156°
140°

Fig. 1. Map of Alaska. Numerals refer to regions described in Table 1.

TABLE 1.

COASTAL ECOSYSTEMS IN ALASKA WITH EXAMPLE LOCATIONS (LISTED IN APPROXIMATE ORDER OF IMPORTANCE)

Types Found	Example Location
Region 1. Southeast Alaska Estimated miles of tidal shoreline = 30,000 = 63% of Alaska Number of types = 21	
Glacial Fiords	Glacier Bay
Turbidity Fiords	Glacier Bay
Rocky Sea Fronts	Sitka
High Velocity Channels	Peril Strait
Medium Salinity Plankton Estuary	Auke Bay
Neutral Embayment and Shore Waters	Sea Otter Sound
Sheltered and Stratified Estuary	Port Frederick
Oligohaline System	Stikine River
Sedimentary Delta	Stikine River
Intertidal Rocks	Pleasant Island
Tide Pools	Pleasant Island
Worm and Clam Flats	Icy Strait
Kelp Beds	Icy Strait
Migrating Subsystem (salmon)	Little Port Walter
Eelgrass and Benthic Algae	Klawak
Bird and Mammal Rocks	Forrester Island
Marshes	Mendenhall Flats
Sewage Wastes	Juneau
Paper Mill Wastes	Silver Bay
Seafood Wastes	Petersburg
Pilings	Ketchikan
Region 2. Pacific Coast, Cape Spencer to Cape Elizabeth Estimated miles of tidal shoreline = 6,500 = 14% of Alaska Number of types = 22	
High Energy Beaches	Cape Suckling
Rocky Sea Fronts	Granite Cape
High Velocity Channels	Bainbridge Passage
Glacial Fiords	Unakwik Inlet
Turbidity Fiords	Columbia Clacier
Medium Salinity Plankton Estuary	Valdez Arm
Neutral Embayment and Shore Waters	Montague Strait
Sheltered and Stratified Estuary	College Fiord
Oligohaline System	Copper River
Sedimentary Delta	Copper River
Intertidal Rocks	Montague Island

Tide Pools	Montague Island
Worm and Clam Flats	Orca Inlet
Eelgrass	Redhead Lagoon
Marshes	Redhead Lagoon
Kelp Beds	Montague Island
Migrating Subsystem (salmon)	Olsen Bay
Bird and Mammal Rocks	Montague Island
Sewage Waste	Cordova
Seafood Waste	Seward
Multiple Stress (earthquake) Beach	Montague Island
Pilings	Valdez

Region 3. Cook Inlet
Estimated miles of tidal shoreline = 400 to 500 = 1% of Alaska
Number of types = 9

High Velocity Channel	Forelands
Sedimentary Delta	Knik Arm
Oligohaline System	Turnagain Arm
Worm and Clam Flats	Cook Inlet
Migrating Subsystem (salmon)	Kachemak Bay
Sewage	Anchorage
Petroleum Shores	Kalgin Island
Pilings	Anchorage
Multiple Stress (ice, oil, tides)	Cook Inlet

Region 4. Kodiak Island, Alaska Peninsula, and Aleutian Islands
Estimated miles of tidal shoreline = 1500 x 5 = 7500 = 16% of Alaska
Number of types = 18

Rocky Sea Fronts	Aleutian Islands
Bird and Mammal Rocks	Amak Island
High Energy	Unimak Bite
High Velocity Channel	Unimak Pass
Neutral Embayment and Shore Waters	Cold Bay
Medium Salinity Plankton Estuary	Kitoi Bay
Sheltered and Stratified Estuary	Kodiak Island
Migrating Subsystem (salmon)	Cold Bay
Worm and Clam Flats	Cold Bay
Kelp Beds	Shumagin Islands
Eelgrass	Kinzarof Lagoon
Marshes	Kinzarof Lagoon
Intertidal Rocks	Aleutian Islands
Tide Pools	Aleutian Islands
Seafood Waste	Kodiak
Petroleum Shores	Amchitka
Pilings	Kodiak
Radioactive Stress	Amchitka

Region 5. Bristol Bay to Bering Strait
Estimated miles of tidal shoreline = 1800 = 4% of Alaska
Number of types = 14

High Energy Beaches	Kudiakof Island
Sedimentary Delta	Yukon Kuskokwim
Oligohaline System	Yukon Kuskokwim
Migrating Subsystems (salmon, birds)	Bristol Bay
Eelgrass	Izembek Lagoon
Medium Salinity Plankton Estuary	Kvichak Bay
Ice Stress Coast	Norton Sound
Under Ice Plankton	N. Bering Sea
Marshes	Izembek Lagoon
Worm and Clam Flats	Izembek Lagoon
Bird and Mammal Rocks	Pribilof Islands
Seafood Wastes	Port Moller
Sewage	Nome
Dredgings	Norton Sound

Region 6. Bering Strait to Canadian Border
Estimated miles of tidal shoreline = 1000 = 2% of Alaska
Number of types = 13

Ice Stressed Beaches	Elson Lagoon
Sea Ice and Under Ice Plankton	Arctic Ocean
High Energy Beaches	Pt. Barrow
Multiple Stress Beaches (ice, light, salinity)	Kasegaluk Lagoon
Oligohaline System	Kotzebue Sound
Sedimentary Delta	Colville River
Bird and Mammal Rocks	Cape Thompson
Worm and Clam Flats	Kotzebue Sound
Sewage	Kotzebue
Marshes	Selawik Lake
Eelgrass	Shishmaref
Kelp Beds	Wainwright
Radioactive Stress	Kotzebue Sound

However, some appear to be in their original state and must be studied as such so that implications of future stresses can be understood. Northern ice stressed systems are particularly vulnerable to man's activity and should therefore receive immediate attention. With the rapid development of the petroleum industry now in progress in arctic North America these systems will rapidly be receiving stresses caused by industry.

More specifically the scientific community should address itself to collection of background data pertinent to knowing what the level of world-wide, regional, and local contamination of coastal systems is at the present time.

Suspicious chemicals represented by three major classes should receive attention: 1) insecticides, herbicides, unique drugs, detergents, or other organic artifacts of man uncommon to the environment; 2) naturally occurring heavy metals such as Pb, Hg, Cd, Os, Be, etc. on a worldwide basis, and elements essential to or involved in metabolism but toxic in high concentrations such as Cu, Zn, Sb, Cr, etc. (the latter are important largely on a local basis); and 3) inorganic elements unnatural or highly increased by man's activities and the whole suite of inorganic elements resulting from fission or induced radioactivity.

Methods of detection of effects of contamination on biological communities is perhaps the area of our greatest weakness and need. When does a contaminant become pollutant? How can subtle, yet damaging, changes in a resource be detected, identified to its extent, and sound judgment be made as to its consequences? Sophisticated methods need to be developed to assess the level of a contaminant or combination of contaminants which limit the metabolism of a specific organism in a community or communities as a whole. Such information would be a signal to potential eutrophication, species diversity, and ultimate damage.

Closely connected with the above is a need for better knowledge of dispersion, both horizontal and vertical transport, and of flushing (exchange) of estuarine systems. The biggest problem here is the lack of techniques that can be used to adequately assess these parameters. Even the problem of current measurements, pertinent to the above, is not fully solved, although much progress is being made in this regard. Remote sensors which can be safely placed in estuaries and be depended upon to give reliable information are badly needed. Vertical transport is a basic parameter that needs measuring, yet no satisfactory method has been devised to cope with this problem. Developments in these areas are essential before an understanding of the physics of estuaries can be realized.

There is also a need for studies of the continental shelf. The deep oceans are fairly well understood or at least methods for their study have been developed. This is not true of the important continental shelf.

Transport of water and interaction with sediments and the atmosphere are poorly understood on the continental shelves; yet, these are the connecting link between the source of contaminant and ultimate dispersal in the deep ocean. While the capacity of the deep ocean to handle wastes is great, the problem is transport.

There is also a lack of that information needed to understand the effects of physical stress on coastal environments. For instance, little is known of the effect of ice and icing conditions on the ability of the environment to handle waste materials. In fact the stress of long periods of darkness or sequential light which occurs in polar regions has been little studied. These areas are gaining importance in the scheme of things in the world and we need to know how photosynthetic organisms live during long dark periods, how organisms cope with long periods of below freezing temperatures and, conversely, how the same organisms manage under high light and temperature conditions. These questions and many more need to be answered before extensive alteration of the environment is brought about by man's activity.

Part IV

GENERAL RECOMMENDATIONS

In the following chapters we examine the status of knowledge of estuarine ecological systems considering types one by one, their distribution in the United States and interactions with man. Whereas the knowledge about the organisms, sediments, water currents, chemical constituents, and other components taken separately is very great, treatment of the parts together as whole systems has been infrequent. Many of our chapter authors were forced to combine fragments from many sources to suggest the operations of the ecological systems assigned to them. We do not yet know enough about most systems for resource management. All too often the cause of some change such as loss of a species population is erroneously assigned to some immediate cause rather than to the ultimate cause that may be several steps removed in the chain of ecological interactions. For example, a species disappears and a disease found to be killing the declining stock is blamed. Both phenomena may, in fact, result from a change in the circulation of nutrients in the estuary which is leading to the replacement of one ecosystem by another. On the basis of the work cited in the Chapters to follow and with the ultimate aim of understanding enough of the main features of whole estuarine ecosystems to predict the consequences of proposed programs of action we give next some recommendations for extending our national and international capabilities in marine ecology and ecological engineering of the coastal ecosystems. In these recommendations we regard man as a part of many ecosystems and in commerce with others. The task before us is management of harmonious systems of man and nature for stability and survival.

Need for Management of Estuaries as Systems

Any plans for the successful development, management, and regulation of estuaries of the United States must be consistent with the ecological and economic principles by which such systems operate with and without modern man. Because the systems of the water differ from the systems of the land in having moving fluid, the land laws do not provide for sensible management and new laws must be enacted to recognize the limitations and requirements of marine systems.

Principle of the Circulating Body as Management Unit

An estuarine system receives its causal energy from three main sources: a) the sun's energy that enables the plant's food-making processes to support living components; b) the organic matter from the rivers which supports other living components; and c) forces of wind, tidal motion, and current which circulate the water and with it the necessary chemical substances, the planktonic microscopic organisms that constitute the estuarine farms, and the gases, oxygen and carbon dioxide, whose regular flow is necessary to all the chemical and biological processes of the estuary.

All these processes control both the natural industry of the bay and the systems that develop when man puts in and takes out materials. Thus the phosphorus, nitrogen, and other fertilizer elements necessary for the growth of microscopic green crops of the estuarine farm are recirculated from the waste products of the clams, fish, and billions of planktonic animals (water flea size) of the area. These biological systems support the aesthetic quality of the bays and their margins, regenerate minerals from wastes (even some from man, but not too much), and keep the bay systems supplied with adequate oxygen. Because of their shallow character, such systems serve as nurseries for juvenile fish, shrimp, and other marine forms that make their fastest growth before migrating out to sea where they support commercial fisheries.

A farm on land stays put and one may buy or sell its productive essence. A farm in an estuary swirls with the water. Title to a piece of the estuary bottom would not confer title to the essence of the bay since it is swirling and exchanging within its natural circulating unit. The first principle, therefore, is that for estuarine management, planning, regulation, and development, no plan can succeed unless it first defines the estuarine circulating unit as the management unit. These units are sometimes defined by physical constrictions and bars in the estuary; at other times they are defined by the way the water behaves, forming up and down circulations that hold plankton and characteristic nutrients as intact masses. The boundaries of the water masses may be changed by building barriers, although making bays smaller may diminish circulation energies and thus diminish the productive power of the system.

As an example, take the Albemarle Regional Planning Program in North Carolina in 1967. Their maps showed their boundaries right across a marine bay as if it were a piece of still land. This is unworkable because any planning done on one side of the bay will be negated if something contrary is done to the same circulating water on the other side of the bay. It is possible to zone marine waters but only if natural units or man-made circulatory barriers are used. Any new legislation must allow possession or authority over units of system circulation if management is to be scientifically sound. For those systems, which by migration export or import shrimp, crabs, and food fish to or from the open sea, there must be provision for management of the two areas together. Thus the subsystems are tied together into larger systems.

The Need for Detailed Ecosystem Maps For Each State

Small scale maps were prepared in our state interviews marking some examples of each type of ecosystem occurring in each state, but making no attempt to map them in detail. These maps (Part III-A) suggest the possibilities for detailed large scale surveys by experienced estuarine scientists and managers in each state, possibly in collaboration with a central team that can maintain some uniformity in symbols and presentation. These maps should refer not only to rigidly fixed systems such as clam flats but should recognize gyrals of circulation which serve to hold the integrity of plankton ecosystems and indigenous production. In the same sense that most states have soil maps, geologic maps, maps of vegetation, or land use maps, the coastal regions need these maps of marine ecosystems and subsystems.

Need for Recognition and Study of New Ecosystem Types

With the creation of many kinds of industrial waste flows, the types of new marine ecological systems possible are far more than the few represented by chapters in this report. It was one of the purposes of the state interviews to locate small marine estuaries which might be receiving new kinds of waste in isolation so that the estuary might provide an example of the kind of ecological system that develops with each waste. What we found in state after state was a pattern of many kinds of waste disposal into the same bays and harbors so that it was not possible to define a case history for scientific purposes. The search for these should continue. Many waste types such as metal plating waste and textile dye wastes, whose stream patterns are known, were not detected alone in the estuaries. The aid of industry in locating these wastes should be sought. Estuaries receiving waste over a number of years may have developed workable ecosystems which can be transplanted. Experience with these new systems should help other industries with similar wastes.

Need for Lagoon Size Microcosm Studies of New Waste Types

Long used in the laboratory, the ecological microcosm is a small model system arranged to have the same inputs and outputs of light, temperature, and chemical flows as real systems in the field. The model is seeded from the real one and somewhat restricted ecosystems develop, with many of the basic properties of the field system. Especially where the consequences of a waste are initiating new ecosystems or modifying old ones, marine microcosm studies on a scale sufficient to include the fishes should be attempted. Such study lagoons are being attempted by staff members who have contributed to this report. Horton and Hobbie operate waste lagoons connecting with the estuary in their studies of effects of phosphate wastes. Odum, Chestnut, Kuenzler, and associates operate marine ponds receiving treated sewage at Morehead City, North Carolina. Rounsefell & associates (Zein-Eldin, 1961) studied a lagoon at Galveston into which copper ore was placed. These approaches allow a test of realistic interactions of whole ecosystems with wastes. Microcosms are small enough to allow replication for effective statistical vertification of tests and if arranged with connection to the real bays, they are large enough to have population pressures from the real system.

Need to Explore New Waste Treatment Processes by Domestication of New Ecosystems

The treatment of waters and wastes often involves captive ecosystems in concrete, which is an apt description of a sewage treatment plant. With so many kinds of ecological systems to consider for waste treatment, why do we stick to so few types. Why do we not domesticate some more types and help the self design processes combine species in unique new groups capable of new waste treatment processes for new waste types.

For example, a beach is really a kind of filter bed which has characteristic organisms that are highly effective in mineralizing and clearing wastes from beaches. The intake to Marineland of the Pacific, drawing water through a beach of coarse sediment utilized an existing system for clearing sea waters. How about other systems such as marshes, underwater grass beds, oyster reefs, and so forth?

Need to Evaluate the Stress of Fluctuating Waste Distributions

The characteristic pattern in American estuaries now is patchiness of many kinds of poorly mixing wastes, stressing organisms first with one condition then another. Whereas plants, micro-organisms and animals can adapt by physiological change or by species substitution to many changes such as increased temperature, they cannot readily adapt to many special conditions at once. Wastes that are now released irregularly or into bays so as to form lenses and patches may be processed so as to provide steady conditions to which organisms may develop new and special adaptations. The importance of the variation in waste releases of one or more kinds needs to be tested and the stress of variation measured in terms of variety and mass of organisms that can be supported.

Need to Use Shellfish Coliform Data for Mapping Eutrophication

Because of the early recognition of the danger to health of pathogenic micro-organisms in estuaries being concentrated in oysters and clams, there have been extensive monitoring programs in the states with restrictions on food harvesting from areas receiving intestinal bacteria from man's wastes. An opportunity exists to use the pattern of coliform bacterial distributions as an index to the nutrients which have been distributed at the same time.

Need for Study and Resource Management by System Rather than by Species

It has been a strong tradition in many state organizations to make ecological surveys and consider the processes in a whole bay, often assigning a state biologist to that bay or region. In the Federal Government until recent years the organization of research and administration has been species oriented. This is partly because many biological scientists have been taught to isolate a species and separate all factors from the problem except the one under concern in order to isolate experimentally the effects under study. Partly it is because legislators and administrators have been unaware of the delicate dependence of larger species of fish and shrimp upon the microscopic food chains and mineral cycles. Partly it is because a generation of fishery biologists were taught population dynamics of single species based on the premise that the rest of the environment was a steady property. The single species approach is important and possibly necessary, but has little predictive value where, for example, the decrease of one species is releasing resources that cause another to increase.

Our surveys cite important data obtained in recent years by broader estuarine study programs of the Federal bureaus as well as by the states. This trend must be accelerated. Farmers would understand that the most practical way to get good cattle is to develop a good food range and then channel the food to the desired animals. Our estuaries are similar. The most practical way to use the sea's biological resources is to maintain a good production range and channel the harvest, whether the food base is algae, bottom plants, or organic matter flowing down river. The adequate management of our estuaries on ecological principles may require changes in the structure of governmental bodies and recruitment of staff with an appreciation of the systems interactions. Programs organized by system may also correspond more closely with those of the corresponding state organizations.

Need for Return Payment to the Estuarine System

It is a taken-for-granted principle in the economy of man that payment is made for goods and services and that such flow of currency allows each industry of the economy to maintain competitive survival. No person or industry is asked to provide some of its production for nothing since this would cause it to be competitively excluded. The principle applies equally to the management of natural systems. Man receives from the bay system and its components the yield of aesthetic recreational restoration, foods, services in processing wastes, and other profits. If we draw on these systems without returning some exchange of special value to the estuary, we cause the aspects in which we are expecting continued yield to be diminished. A formula must be derived by which services that stimulate bay processes, such as encouraging desirable fish food chains, should be returned to the bay in proportion to the dollar yield from these bays. Such programs will insure that the bay becomes part of the economy of man and nature rather than a mining operation in which the bay soon has no further use for sustaining a viable coastal basis for human development. The feed back payment principle is shown in Fig. 1. How much effort is necessary to pay the estuary enough to encourage more growth of the type being harvested? There are precedents for this kind of program. For example, some of the Federal laws provide monies to stimulate sports fishing in proportion to the monies derived from licenses to take fish.

Need for Enabling Mechanisms for Sea Harvest and Farming at Least Cost

Partly because of the history of competition of sports and commercial fishing, partly because legislators believe that little fishes if left to grow survive to become as many big fishes, and partly out of tradition, all kinds of restrictions are placed on the farming and harvest of the waters, which would seem absurd if placed on the cattle farmer. The way to control overgrazing is to control the amount of grazing, but not to raise the costs to the grazer. If a body of water is assigned to food production, it needs to be managed for its maximum yields of food. If assigned for sports fishing, carnivore chains need to be maximized. Estuarine zoning may set up one bay for sports fishing and another for commercial fishing. Where resource development is intended, enough title to that system through long term lease or other device is required so that large capital ventures can be made in its management to include whole bay fertilization, stock management, bottom control, etc. The shallow seas can be farmed as water systems. Large bays will require large capital and methods should be proven on very small bays first. Our present system of mixing incompatible competing uses prevents us from attainment of maximum values. Laws to allow management of the estuarine systems as units are required. Shellfisheries cannot be managed by themselves since their food is filtered from the estuarine microscopic farms (organic matter and plankton). The old bottom leasing idea ignored the water which must be managed with the bottom.

Need to Preserve Some Locations with Complexity, Aesthetic Yield, and Water Purity

Where conditons in the estuaries are not severely shocked by changing water levels, salinities, floods, and other disturbances, some very diversified

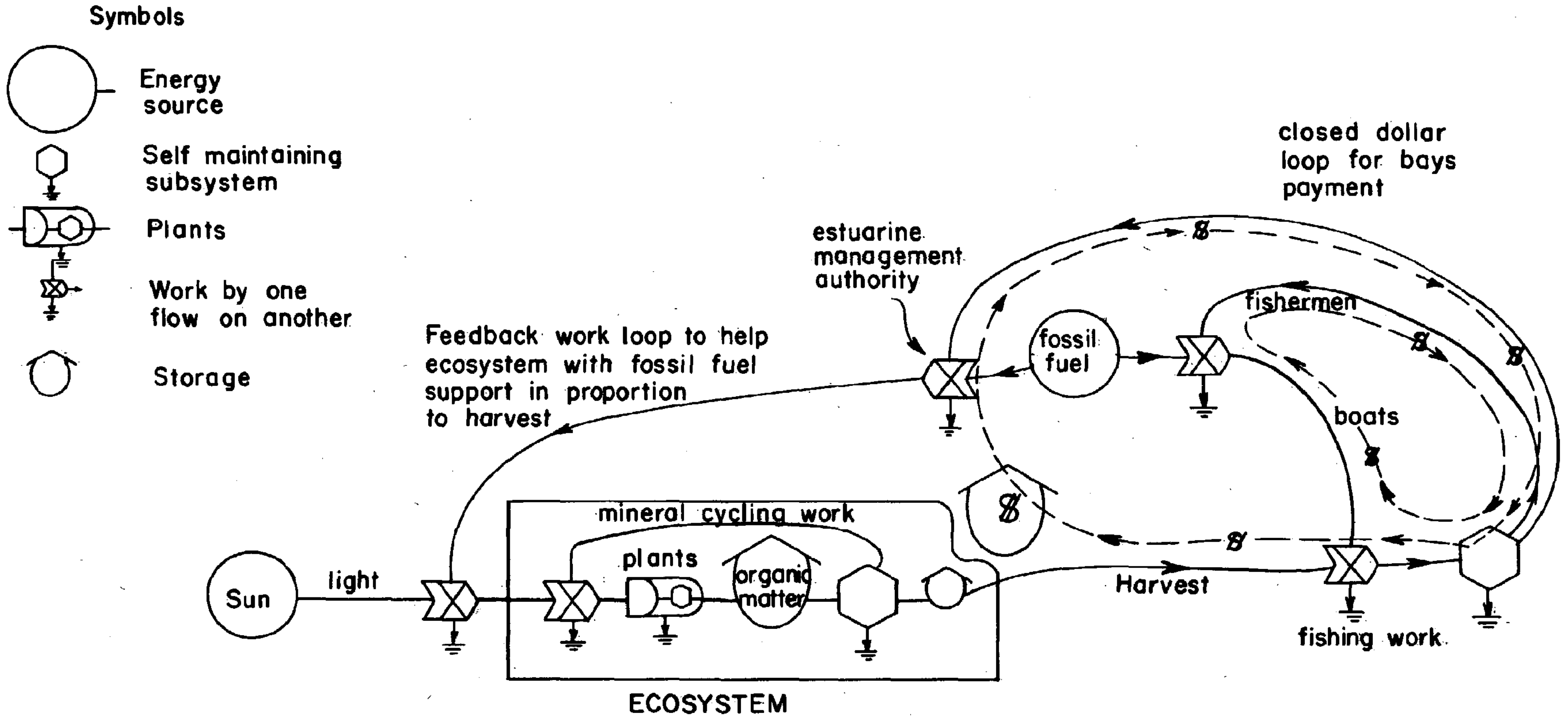

Symbols
Energy source
Self maintaining subsystem
Plants
Work by one flow on another
Storage
Feedback work loop to help ecosystem with fossil fuel support in proportion to harvest
estuarine management authority
closed dollar loop for bays payment
fossil fuel
fishermen
boats
$
Sun
light
mineral cycling work
plants
organic matter
Harvest
fishing work
ECOSYSTEM

Fig. 1. Energy flow diagram with work payment to the estuary for its service to man so as to develop self stabilizing design of man and nature. Note that the currency of humans flows in the opposite direction and by the above arrangement has a closed balance of payments between the fishery users and an authority established to represent the interests of the ecosystem (H. T. Odum).

(in species) living systems develop which have great aesthetic value to the recreation industry. Their associated clarity and purity of waters is due in part to the complexity of living things which are efficient at mineralizing many special chemical substances through organismal specialization. There are the interesting coral reefs in tropical waters, kelp beds in California, intertidal crops in Maine, and grass flats in many other areas. The variety of sea life, ofskin-diving pleasures, or of scientific values cause these areas to be of special consideration since they are easily destroyed with disturbances. These waters are in the class of National Parks and need to be set aside in such a way that the waters that bathe these systems do not mix with the waters serving other uses where there is turbidity, industrial wastes, insecticides, etc. As more and more freshwaters are dammed upstream the floods to the estuaries in many places will diminish and then these complex and stable systems may develop in areas that previously did not have them.

Need to Manage and Increase Areas of Estuarine Nursery

In the management of the estuarine margins, the importance of the marshes, the shallow underwater grassy bottoms, and other shallow waters must be emphasized since this is where enough light penetrates and is concentrated to develop much of the productivity that supports food, sports, aesthetics, and ultimately cleansing power. The deepening of margins and the dredging for small boat channels and waterfront bulkheads essentially destroy these nursery areas because the waters are then deep and turbid enough to exceed the threshold for minimum light that scientists call the critical depth. The swirling, estuarine, microscopic farm is choked dead if the green cells are in the dark too much of the time, just as if a black cover were kept over a terrestrial farm. There are ways to have both marinas and nursery margins, such as by cutting marina into new land, but never at the edge of the bay. In cases of damage already done, regrading of estuarine bottoms to optimum production depth can restore productivities. The cost of this may be included in channel development projects as a necessary payment back to the bay for the special service extracted.

Need to Manage the Total System of Land and Water

The requirements of management of the circulating estuarine water systems are diverse and must be oriented towards many productive aspects of the economy. The past tendency for one user group to gain full control of a bay without due process and ruin it for other uses needs to be prevented in the future by placing regulation and development on a body which is charged to develop the water system for optimum pattern with the lands surrounding. Presently the development of land systems without incorporating the water systems is a conflict of interest in which the public's rights are being given away often as means for attracting industry. Since the states are competing for industry and since the destructive navigational dredging programs are Federal, some Federal action may be necessary. However, development needs the kind of private enterprise one associates with industrial-governmental-agricultural collaboration in terrestrial farming. State enabling laws are needed for full development of all the aspects of the estuaries. Regarding the bays as a development and design responsibility will go a long way toward making state boards of Conservation and Development do positive things to their estuarine resources instead of following the policy sometimes developing by default of encouraging their destruction by permissive attitudes towards industries on land.

Need for Developing Some Kind of Ecosystem for the Multiple Pollution Harbors

In the heavily polluted harbors and urban waste centers found in most states, the nature of the ecological system is uncertain. Studies on the Black Sea, summarized by Kriss, show that a workable productive ecosystem can develop on top of an anerobic, bacteria dominated decomposition pool. With toxicities, fluctuations, and substances of new types, the harbors may not now exhibit such harmony of self processing of wastes. What can be done with these areas? At what level of waste disposal is a functional ecological system able to mineralize? What organisms may be preadapted to such a system? What is the relative cost to the nation of utilizing the harbor waters as decomposition ponds as opposed to construction of waste systems?

Need to Use the Wave, Tide, and Current Energies

Compared to many environments, the estuaries have high productivity of plant and animal growth which may be due partly to high physical energies absorbed from tides, waves, and wind driven currents. The estuary provides means for converting some of this energy into the work of recirculating minerals, larvae, and food substances, thereby raising the levels of total yield. The amounts of these energies that are contributing to the estuarine resource have been measured rarely and the potentials which are available for estuarine management little considered relative to the biological and human uses of the coasts. Research focus is needed to map these energies and relate to their productivities, capacities for waste receival, and other aspects of the systems as a whole. An inventory of energy budgets, including all sources of energy contribution and stress loss, is a means for generalization and management of the whole systems.

Need to Utilize the Competition of Ecosystems

That alternative formulas exist for ecosystems in the same area has long been known by those designing fish ponds. Small differences in the processing of fertilizer nutrients, manipulation of turbidities, and bottom changes can convert a plankton based food chain pond to a pond whose food chain is based primarily on bottom attached plants. Systems tend to maintain their own type by recycling their characteristic nutrient ratios of mineral elements, by supporting larger animals that have behavior programs for eating members of alternative systems, and by other mechanisms. In the management of estuaries we have to learn under which conditions one system displaces another and by what means one system can exert negative influences on another. There is the promising possibility of manipulating the control members of these systems so as to develop the system desired.

Need to Test the Pulse-Reproduction-Migration Theory for Use in Management

Tested in our state surveys and chapters is an ecological hypothesis that explains many complex patterns of estuarine biology and provides a predictive basis for planning and management. In the course of a year there is a rise and fall in the intensity of energy inflow to an estuary as light, organic matter in rivers, and other sources such as waste. A system which becomes adapted and remains stable in a varying regime tends to program its reproductive activities and its migrations so that they correspond to the pulse in food availability at any point in the food web. Even the salmon migrations begin to make sense when one notices that the young, in the most critical periods of growth, are found in estuaries and other bodies at a time when the foods available to them are maximimized. The further north a system is found the greater is the seasonal pulse and the greater the role of pulsed reproduction and migration. The entire system of shelf and oceanic fisheries slides north and south in response to the pulse of the production system and tap outgoing stocks from the estuaries, thus coupling all into a world-wide system of the seas. Many biologists find coordinated patterns at the large ecosystem level difficult to comprehend because their training has been with the organism first, the ecological system being "whatever the organisms do." We would describe the system differently; because of the mineral cycles and the programmatic patterns long since built into the seas, organisms are present which fit the system. They fit the pulse of energy well enough to maximize the total possible energy utilization. The addition of waste release regimes must be compatible and steady so that adaptations are allowed to develop or be retained.

Need for a Federal Role in Research and Development Coordination

Whereas the management of particular ecosystems is well established in state resource management organizations, an opportunity exists for a Federal role in assigning its special grant and contract funds so as to cover the main kinds of ecological systems, at the same time distributing regionally the work load along natural lines. For example, if efforts are assigned in areas where systems are prominent, Georgia and Louisiana might do marshes and oligohaline systems, Florida the mangroves, Puerto Rico and Hawaii the coral reefs, Maine the rocky inter-tidal system, Texas the hypersaline system, California the kelp system, Alaska the fjord systems, South Carolina the oyster reefs, North Carolina the beach systems, etc, etc.

Need for Systems Simulation of Each System Type

For each system, there now are energy and chemical flow diagrams in various degrees of detail and accuracy which permit computer simulation of proposed changes in input conditions. The procedure at our present state of knowledge may be summarized as follows:

Based on field data and knowledge of the species an energy diagram is drawn showing principal pathways of food, work, and controlling chemical flows. The standing quantities in storage in various populations, waters, and muds are indicated. These storages are called compartments. The flow along each pathway is stated in a computer program as proportional to the concentration upstream in the flow diagram. Growth is programmed by feedback from storage to flow. Some daily or seasonal patterns of inflows and outflows for the system are programmed. The program is run and the interaction of all the statements provides graphs with time for all the compartments. These graphs are compared with observed patterns. The discrepancies indicate difficulties in the energy flow model so that it may be modified and tested again. The simulation thus provides a means for testing the consistency of knowledge about the parts with observations about the behavior of the whole. Simulation of one representative example of each type of ecosystem should be attempted now. It may be modified according to specific problems when a realistic program is developed for each system type for purposes of prediction of possibilities.

Need for Compatible Use Plans and Estuarine Barrier Zoning

Because of the mixing aspects, an estuarine unit is defined by the circulation of water and minerals. Plans for use must separate and combine users and uses so that no incompatible uses are operated in the same bay. Thus shipping, bilge waters, poisonous copper bottom paints of ships, industrial wastes, and continuous dredging are not compatible with aesthetic, fishing, food, and purification aspects and should be isolated by barriers so that the waters do not mix. The hot water from large power plants takes the life out of the water that passes through and thus destroys the planktonic estuarine farm. This use may be compatible with the industrial uses but not with the aesthetic-biological ones. The values of the bays are large; for example, about $370/acre per year in Corpus Christi Bay (Texas) in 1960. No one user claimed a preponderance of this value. Proper management may allow some systems for each purpose. The biological-aesthetic ones require large areas of sunlight as do farms. The industrial ones can be concentrated in small bays and channels in the same way that industrial cities are channeled. Water from one must not be circulated into the other. Plans like the following need consideration.

A Zoned-Sector Plan for the Multiple Development of Marine Bays*

H. T. Odum

*This section was distributed as a circular during Legislative discussions in Texas in 1960. Although the examples are from Texas, the zoned sector plan is general.

"This is a proposition for a zoned sector plan for the maximum, multiple development of the marine bays of Texas. With over a million acres of bays behind the beach lines, Texas possesses vast and fertile shallow lagoons. Development of the investment and resource use is accelerating over this new frontier but competitions and conflicts are already retarding progress.

"The value of the bays in their present partially-developed state is already about $370.00 per acre per year as estimated for the Corpus Christi area by Anderson (1960), but the potential values are much greater. In Table 1 are cited present value estimates from Anderson's study.

"Many potential uses and users are excluded because there are no means and mechanisms for permitting harmonious co-existence of state, federal, corporate and individual enterprises. Especially, are there difficulties in acquisition of titles and leases to underwater lands; no agency, no laws, and no authorities are sufficiently broad to cover the multiple aspects of use. Consequently there are no broad plans for maximum development. Instead pressures develop between groups with efforts made to exclude competing users from the bays. Some of the specific uses and some of the conflicts between users are cited in the recent report on Texas Natural Resources by the Houston Chamber of Commerce.

"In Table 2 are listed some examples of the controversies and conflicts developing in Texas recently. From the data on values in Table 1 it is clear that no one interest is of such overwhelming importance to the general economy to permit exclusive use of the bays. On the other hand locally one user may have sufficient concentration of effort and investment and value yield to justify a local dominance. What is needed is a plan to permit the best possible multiple use.

"The proposed plan is based on a partial separation of users and investment leases based on zoning according to the nature of the activity and its effect on the water. By associating those users that can most readily be located together without conflict, maximum benefit can be accrued to the public good while allowing all users some right and position. The overall plan is pictured in Figure 2.

"In sector 1 are located those users of an industrial nature whose operations tend to be harmful to the tourist, fishing, and sports activities. This sector is for industrial use, maintained in deep channels for navigation. Dredging is permitted here for navigation and shell. Waste disposal is received here. Cooling waters are taken from this sector and returned to the sector. The waters of this sector will tend to have minimal life. Fouling of ship bottoms and cooling intake pipes will be minimal. Harmful effects of wastes, bilge waters, copper from ship bottoms and other activity will be restricted to this zone. The discharge from this zone will be directed toward the open Gulf as much as possible leaving the other sectors little affected.

Table 1. Dollar per Acre per Year Estimates of the Bays in the Corpus Christi Area (from Anderson 1960)

	Annual Dollar Per Acre Values
Industrial	
Navigation	64
Oil and Gas	124
Cooling	10
Waste Disposal	?
Shell	5
Sub Total	203
Use Based on Biological Food	
Tourist, Sports	130
Local Residents	21
Commercial Shrimp	13
Bait Shrimp	1.3
Fin Fish	0.34
Crabs and Oysters	1
Sub Total	167
Total	370

Table 2. Some Conflicts and Incongruities in the Marine Bays of Texas

Proposed law to lease bay bottoms at a few cents per acre per year for real estate thus taking value away from present users such as shrimp industry.

Propositions to exclude nets by sports interest.

Proposition to exclude bay trawlers thus putting smaller boat trawlers out of business.

Condemnation of bays for commercial oysters due to sanitary pollution and inadequate control of waste disposal.

Argument as to responsibility of shell dredgers in restoring former reefs.

Payment of money to restore reefs while live reefs are being dredged.

Accusation that bait shrimpers and bay trawlers are taking shrimp stocks while too small instead of waiting for greater value later.

Dredging of navigation channels through rich nursery grounds.

Fight over title to spoil islands.

Argument between oil companies with pipe lines in shell areas and dredgers of shell.

Conflict between duck grounds and dredging of grass flats.

Stopping freshwater upstream affecting salinity, especially oysters downstream in the bays.

Disposal of chemical wastes in conflict with needs of fishing and tourism.

Arguments over effects of passes and new channels on sports fish.

Fights over waterfront right with tide lines varying and in doubt.

Argument over treated wastes and their fertilizing effects.

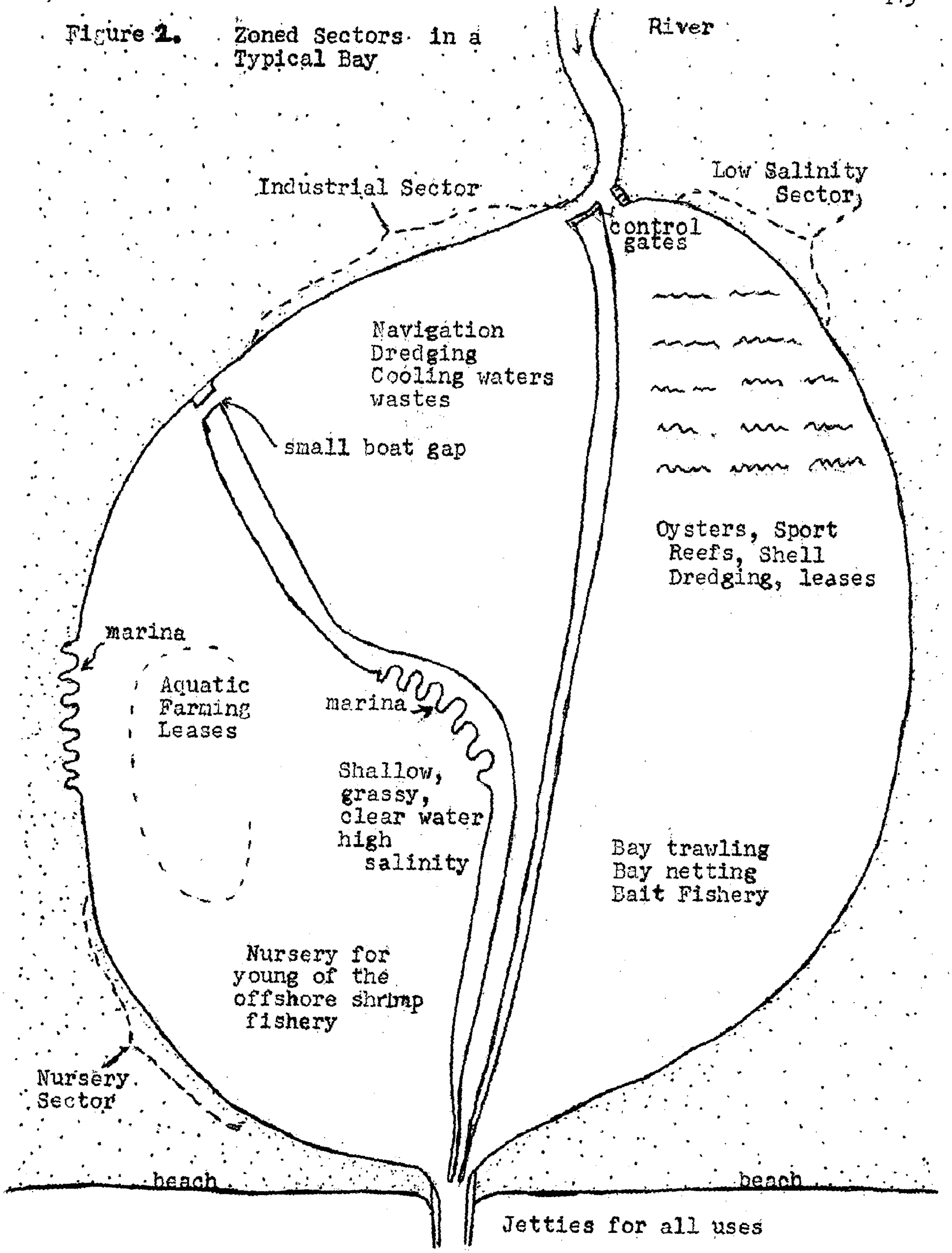
Proposed use of marine bays as freshwater storage to eliminate present uses.

Efforts to increase tourist industry while dredging and pollution eliminate the nearby tourist beaches and fishing grounds.

Attempts to develop a beach facility downstream from attempts to accelerate industrial development.

Conflict over nuisance and odors of excess algae and needs for disposal of treated municipal effluents.

Figure 1. Zoned Sectors in a Typical Bay


River
Industrial Sector
Low Salinity Sector
control gates
Navigation
Dredging
Cooling waters
wastes
small boat gap
Oysters, Sport
Reefs, Shell
Dredging, leases
marina
Aquatic
Farming
Leases
marina
Shallow,
grassy,
clear water
high
salinity
Bay trawling
Bay netting
Bait Fishery
Nursery for
young of the
offshore shrimp
fishery
Nursery
Sector
beach
beach
Jetties for all uses
Open Gulf

Whereas this diagram satisfies some zoning objectives, it reduces wave and current energy, lowering productivity.

"Sector 2 is the low salinity sector to contain the mouth of the river. Such water as may be allowed from the overall river basin plans upstream will thus be conserved in a relatively small area to permit an oyster industry and live oyster reefs so attractive to sports fishing. Oyster reefs of Texas must have brackish salinity. The oyster reefs are realigned into neat rows across the current for maximum growth, for ease of management, lease, and access and also to permit removal of dead shell from the inter-reef areas. This sector will be turbid due to river contributions and dredging and will not allow maximum light penetration necessary to best growth of fish food and shrimp larvae. Being of moderate depth the area will maintain populations of larger species migrating from shallow areas. Some nutrition to the food chains is derived from the river inflows. A zone in this sector should be reserved for netting and trawling of boats too small to work regularly in the Gulf. It is a premise of this plan that none of the marine resource users can or should be excluded from the public resource by some other group with more political power. Instead conflicts or imagined conflicts can be solved by zoning to provide adequate area for each user large and small.

"Sector 3 is the shallow clear nursery sector. Both polluted waters and the turbid river waters of varying salinity are excluded from the broad shallow areas, so that rich beds of grass may develop with maximum plant growth and nutrition for the food chains that provide maximum yields of fish, crabs, and shrimp. Part of this area is arranged and leveed for aquatic farming leases for underwater grass for cattle and shrimp, crabs, food fish, and fish for the animal food industry. Another part is reserved as an inviolate nursery sector for the offshore shrimp industry. Although the eggs are believed deposited outside, the microscopic larvae come into the nursery grounds to grow up before going back out into the Gulf where they are caught. This sector is also for duck hunting since grassy areas are part of food attraction. The shallows allow blinds to be put up.

Administration of the Plan

"No existing agency except the legislature now has the breadth of authority and interest to initiate a positive program such as required by the times for the full development of the sea frontier. Some kind of enabling action by the legislature is thus the first step. Some appropriation and fiscal structure will be necessary as well as some engineering division for construction and maintenance. The unit for planning must include the whole of a bay system if the zoning is to be effective in separating conflicting users. It may be that 8 bay marine resource development districts (Sabine, Galveston, Freeport, Matagorda, San Antonio Bay, Corpus-Aransas-Copano, Upper Laguna-Baffin, Lower Laguna) can be formed corresponding to the 8 natural areas. Another alternative for administration may follow enabling legislation to permit users of harmonious association to create their own barriers consistent with overall zoning. In any case some way must be found to permit the same kind of enterprise in the marine waters as on the land. It goes without saying that the idealized plan in Figure 2 does not fit any particular bay exactly and that the zoning and barriers must be adapted to local situations."

Difficulties

Where tides are small, dividing bays with dikes diminishes circulation, causing silting to more shallow depths, and some data suggest that productivities are reduced. Zoning needs to be arranged without eliminating the large circulation energies of wind and tide or preventing access of migrating populations.

Zoning Example, Georgia

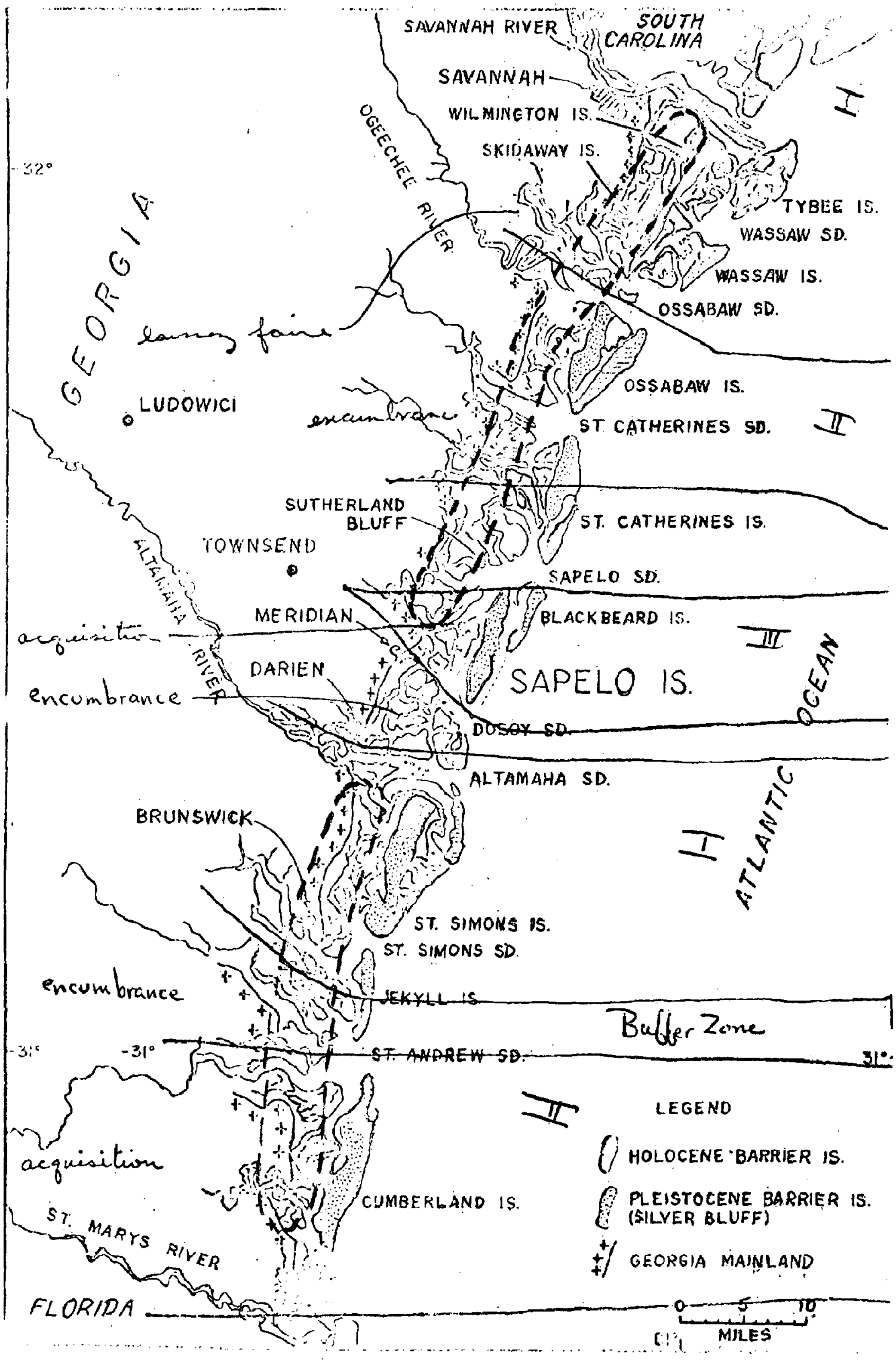
The possibilities of Marine Resource Zoning are illustrated by Fig. 3 supplied by Eugene P. Odum, University of Georgia, from some discussions underway in 1969. A general statement of Marine Zoning ideals was given by E. P. Odum (1968). Since productivity of above-water marsh grass is so great, it was proposed that the productive heart of the tidal marsh be reserved against other exploitation as a "marsh bank" in the same sense as the federal "soil bank" program. See dotted loops in Fig. 3.

Need to Utilize Natural Experiments

In the management of large estuaries, manipulations are very expensive. If action programs are instituted they should be identified as an example of a class of actions and studied before and after the change so that we obtain guidelines for future propositions of this class. For example, James T. Darby and Clair P. Guess of the South Carolina Water Recources Committee have written us of the upcoming opportunity to compare an estuarine system in South Carolina with and without a heavy river discharge. The Santee River which has been discharged through Charleston Harbor since 1941 may be soon returned by engineering projects to its former channel further north to decrease silting. Will total food harvests and recreation yields increase or decrease? Another example is the bypass ship channel into New Orleans through oligohaline Lake Borgne. Whereas over a hundred thousand dollars of federal funds were spent on studies before dredging and duly reported, where are the published details of the conditions which exist now after the canal was dredged? The piecemeal, immediate - crisis approach in federal agencies under the guise of economy is costing America large sums. The opportunities to find answers applicable to management of each class of ecosystem problems is lost because budgetary subdivisions sometime do not recognize it as their responsibility to follow through with published before-and-after comparisons.

Need to Mix Organismic Biology with Systems Synthesis

Represented by the new book by Green (1968) on the estuarine animals or by the Organismic Biology Research program at the Marine Biological Laboratory at Woods Hole, Massachusetts are studies of important species and their role in the ecological system. They include life cycles, distributions, seasonal regimes, food habits, predators, and responses to various factors as


SAVANNAH RIVER
SOUTH CAROLINA
SAVANNAH
WILMINGTON IS.
SKIDAWAY IS.
OGEECHEE RIVER
TYBEE IS.
WASSAW SD.
WASSAW IS.
OSSABAW SD.
32°
GEORGIA
laissez faire
LUDOWICI
OSSABAW IS.
encumbrance
ST. CATHERINES SD.
II
SUTHERLAND BLUFF
ST. CATHERINES IS.
TOWNSEND
ALTAMAHA RIVER
SAPELO SD.
MERIDIAN
BLACKBEARD IS.
acquisition
III
OCEAN
DARIEN
SAPELO IS.
encumbrance
~~DOBOY SD.~~
ALTAMAHA SD.
BRUNSWICK
I
ATLANTIC
ST. SIMONS IS.
ST. SIMONS SD.
encumbrance
~~JEKYLL IS.~~
Buffer Zone
31°
-31°
~~ST. ANDREW SD.~~
31°
II
LEGEND
HOLOCENE BARRIER IS.
PLEISTOCENE BARRIER IS. (SILVER BLUFF)
GEORGIA MAINLAND
acquisition
CUMBERLAND IS.
ST. MARYS RIVER
FLORIDA
0 5 10
MILES

I Industrial, port and waste disposal

Fisheries, Recreation Hunting

Doubtful

Research

Buffer zone

Industrial, port and recreation with limited waste disposal

Wilderness preserve or sea shore park and fisheries

Fig. 3 Suggested zoning for Georgia from E.P. Odum(1968). Dashed loops are "marsh bank reserves".

tested in laboratory controlled experiments such as temperature, salinity, photoperiod, wastes, etc. In some examples where the diversity is small as with gribbles boring in treated wood, the organismic biology includes much of the ecosystem, but in complex systems such as coral reefs the single species study involves a small energy fraction and does not provide predictability about the organisms in nature because their interactions with each other, their mineral cycles, and food chains depend mainly on other species. The organismic approach has a long honored tradition and there is much more to be done to understand even the species which are of sports and commercial interest, but the management of the ecosystems requires an understanding of the behavior of the combinations interacting and it is the direct experimental study of the system that may be the important focus needed. This may be done by adding specialists in systems synthesis to the species teams. The Smithsonian Institute's efforts to add ecology to its species-oriented traditional approaches is an example of this approach in recent years.

Need to Program Man's Estuarine Interactions Over Longer Periods and Wider Areas

The self-designing feature of ecological community adaptations are continuously demonstrated along the coasts as populations in one area make temporary excursions and invasions of areas outside their main range in larval swarms and individual migrations and as temporary colonies. The green crab and blue crab in Maine make inroads and take losses that are in part correlated with temperature. The eastern oyster makes northward invasions into the vicinity of Cape Cod in some years. The areas of substitution of one species for another in the same niche or the division of one niche among more than one species may expand and contract from one year to another in response to weather variations or a wave of effect spreading from population-dense areas.

Our present means of planning, authorizing research, and concocting action programs may respond in a too sensitive manner to the rise and fall of biological stocks in local places. Local changes in patterns over a 20 year period may be reasonably normal and predictable at least statistically. Many natural stocks provide for such variability with large year class storages. Man's planning, his capitalization of fisheries and recreation investments must also provide for long range stability. This can be done by larger storages to even out local variations, by coupling local utilizations to each other over larger geographical distances in the same way that the natural populations are coupled by shifting stocks in migration. Zones of central virility may move as needed distributing the gains and liabilities over larger areas and times as one does insurance.

Need to Unite Scientific and Economic Approaches

C. P. Snow's two intellectual worlds, one of natural scientific tradition and one of social science tradition need to be united by training more people in both traditions each learning languages of the other well enough to use them. Better yet the new trainees should learn both. In our survey we find documents from the two backgrounds like two different worlds, dealing with the same estuarine resources sometimes quoting each other in a perfunctory way, without really using the results. For example the book on Ocean Fisheries by Christy and Scott (1965) or the coastal plains economic study by Hite and Stepp (1969) attempts to understand fisheries as an economic system, without the biological system showing. This has as much chance as the converse study of biology of fisheries systems without including the inputs and outputs of man's economy. They are both parts of the same system. In this study, our original proposal authorized some synthesis of the economic and ecological, but the administrative requirements for specialization caused an amendment to be issued later eliminating the economic synthesis from our effort. One cannot understand systems by breaking them up into parts unless one also has quantitative ways and a large expensive effort at putting the parts together again.

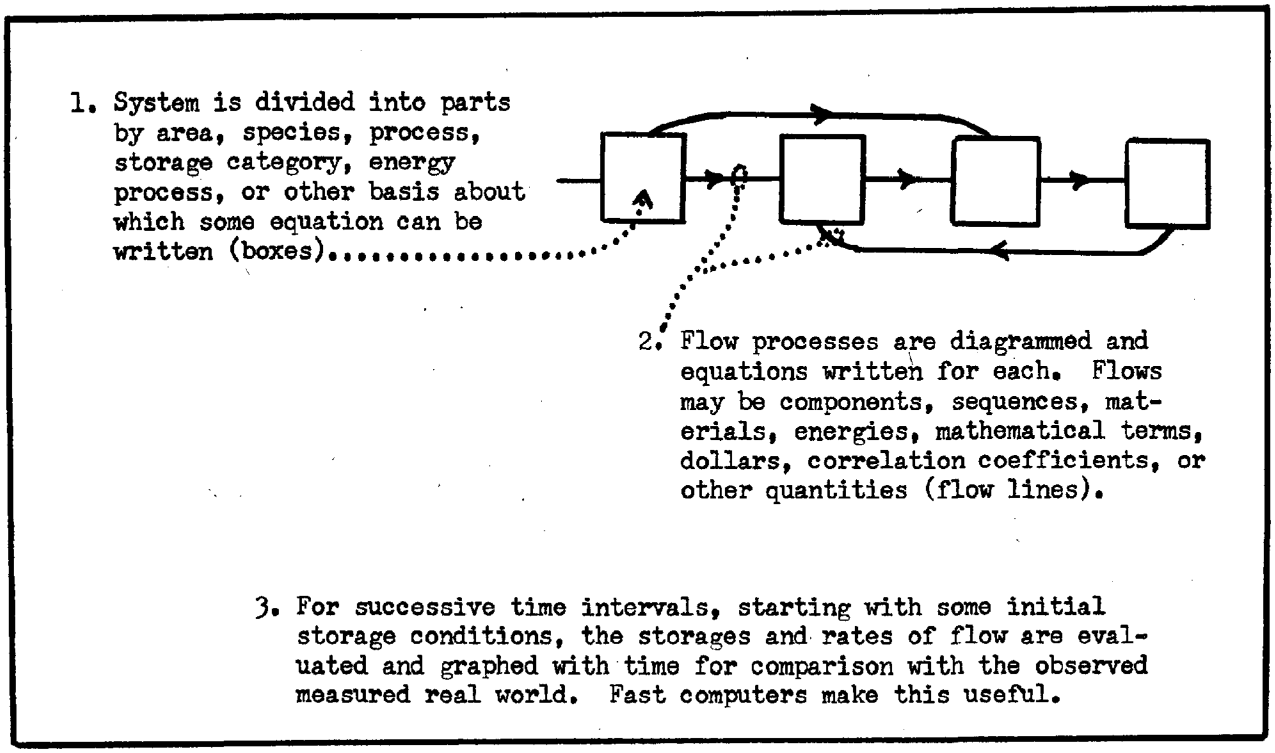
Energy-Dollar Calculation

In addition to these dollar values we estimate the value of the work the ecological system is doing outside of man's dollar economy. With productivity and metabolism at about 5 g dry matter/m^2/day and 4 kcal/g there are about 29 x 10^7 kcal/acre/year of work processed in maintaining a useful part of the earth's life support. At our approximate rate of 10,000 kcal work per dollar, the equivalent money value is $29,000 per acre per year. As life support systems become scarce we might ponder the meaning of these high values.

Systems Analysis and Total Systems Study

Finally, ten years after its use in other fields, there are effective beginnings in the systems analysis of estuarine systems. One might cite the Stanford papers on simulation of production and oxygen patterns from knowledge of component processes (McCarty and Kennedy, 1967). The versatility of systems analysis approaches is suggested in Figure 4.

Showing through simulation how the parts produce the patterns of the whole may help with management of the species as parts as well as of whole estuaries. However, the study of whole systems may not necessarily require this kind of systems analysis that isolates the parts and resynthesizes them. Soon for each type of system general organization, structure, and temporal behavior are learned. We may learn to recognize and predict the responses of whole systems to various treatments if they are considered by type as defined in our report. A systems analysis of the parts may then be replaced by knowledge of overall performance for each class of system. Often the program of the whole is what is required for management. We return to our theme of classifying the coastal ecological systems including those resulting from human participations. Through knowledge of the behavior of ecological systems, can we not plan for and manage a better biosphere?



1. System is divided into parts by area, species, process, storage category, energy process, or other basis about which some equation can be written (boxes)..................

2. Flow processes are diagrammed and equations written for each. Flows may be components, sequences, materials, energies, mathematical terms, dollars, correlation coefficients, or other quantities (flow lines).

3. For successive time intervals, starting with some initial storage conditions, the storages and rates of flow are evaluated and graphed with time for comparison with the observed measured real world. Fast computers make this useful.

Fig. 4. Systems Analysis.

Part V

Chapter A-1

ROCKY SEA FRONTS AND INTER-TIDAL ROCKS

Rocky sea fronts and rigid man-made surfaces that stand against waves in the inter-tidal zone develop characteristic attached ecosystems in bands above and below the water level. Breaking waves, intermittent exposures to heating and drying, and problems of maintaining two regimes of gas exchange drain energies from other potentials by requiring special adaptations for mere existence. However, the moving water provides renewal of nutrients and food, aeration, and partial protection from carnivores, adaptations which maintain dense masses of animals. The balance of special conditions associated with the water level produces characteristic bands of attached organisms such as algae, mussels, limpets, chitons, and urchins in crevices (Figs. 1-4). The rocky sea front has some properties in common with the high velocity surface systems (Chap. A-3) such as high metabolic rate and concentrated food flows, but the inter-tidal surfaces have zonation associated with vertical light fields, frequency of wetting, amount of spray, hours of exposure to underwater food and carnivores, and wave swashing of filamentous algae that act as a scouring broom. Communities may develop on rocky shores built by geological processes or on calcareous surfaces built by the plants and animals themselves.

Variation and species substitution occur with latitude as tide and air mass exposures change, although the variation in the form of the encrusting systems on rocky coasts may be less than in more uniform environmental situations. Periwinkles, for example, characterize the upper splash zones. Small Littorina ziczac on tropical sea fronts is replaced farther north by other species of the genus.

Like marshes the intertidal rocky subsystems may be important to the producing, consuming, and cycling components of the estuary. In the United States the intertidal sea front is often a neglected resource with potentialities for greater use of algal beds and mussels, and for the trapping of fish and crustacea that move into these beds with the tide.

EXAMPLES

Cool Sea Fronts of the West Coast

Hedgepeth (1967) provides a diagrammatic view (Fig. 1) and an introductory account of rocky shore zonation. Fig. 2 from Kirk (1962) shows other views of principal members of rocky shore ecosystems from the Washington coast. Principal members from the southern California coast are shown from Emery (1960) in Fig. 3.

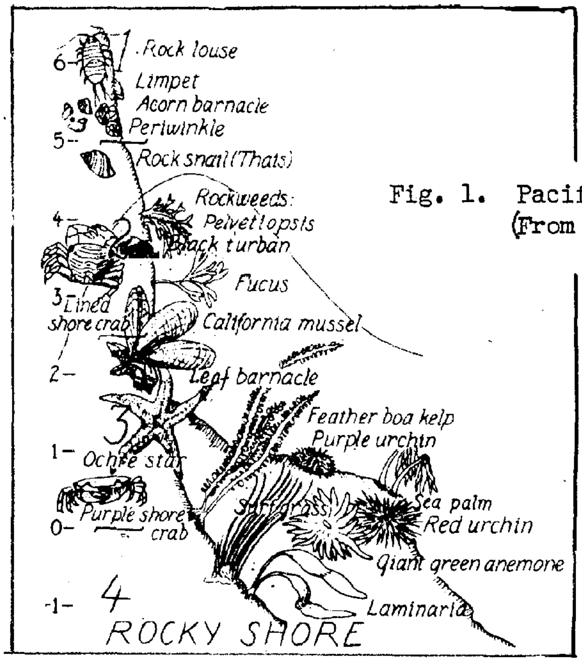

6
1 Rock louse
Limpet
Acorn barnacle
Periwinkle
5
Rock snail (Thais)
Rockweeds:
Pelvetiopsis
4
Black turban
2
Fucus
3 Lined shore crab
California mussel
2
Leaf barnacle
Feather boa kelp
Purple urchin
1
Ochre star
3
Purple shore crab
0
Surfgrass
Sea palm
Red urchin
Giant green anemone
-1
4
Laminaria
ROCKY SHORE

Fig. 1. Pacific Coast rocky zonation (From Hedgepeth 1967b).

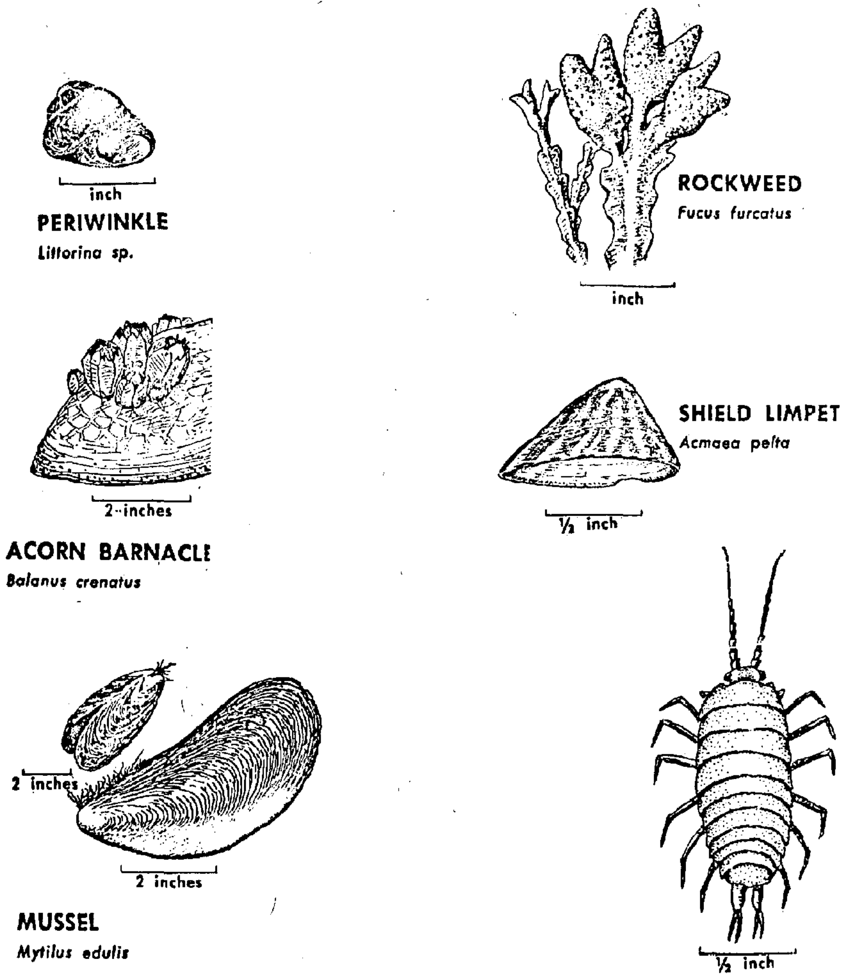
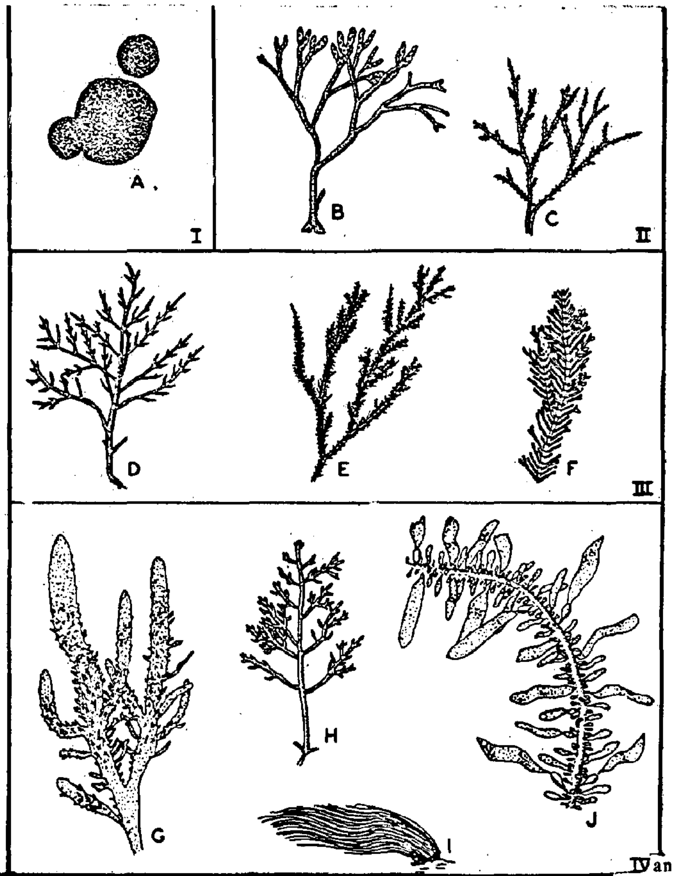

inch
PERIWINKLE
Littorina sp.
ROCKWEED
Fucus furcatus
inch
2 inches
ACORN BARNACLE
Balanus crenatus
SHIELD LIMPET
Acmaea pelta
½ inch
2 inches
2 inches
MUSSEL
Mytilus edulis
½ inch

Fig. 2. Rocky Coast animals of the Washington coast (From Kirk 1962).

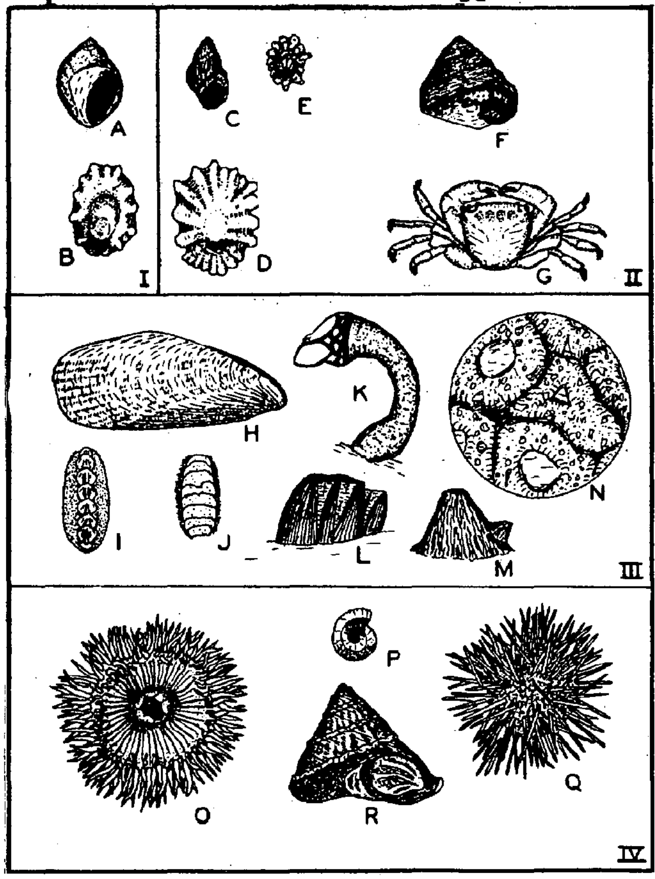


Some common plants of rocky shores in southern California. I, wave and spray zone: A, *Ralfsia* sp. (×0.04).

II, high-tide zone: B, *Pelvetia fastigiata* (J. Ag.) De Toni (×0.09); C, *Endocladia muricata* (P. & R.) J. Ag. (×0.5).

III, midtide zone: D, *Gigartina canaliculata* Harv. (×0.15); E, *Gigartina leptorhynchos* J. Ag. (×0.15); F, *Corallina vancouverensis* Yendo (×1.5).

IV, low-tide zone: G, *Gigartina spinosa* (Kutz) Harv. (×0.04); H, *Gelidium cartilagineum* var. *robustum* Gardn. (×0.15); I, *Phyllospadix torryi* S. Wat. (×0.02) (habit); J, *Egregia laevigata* Setch. (×0.1).



Some common animals of rocky shores in southern California. I, wave and spray zone: A, *Littorina planaxis* Philippi, periwinkle (×1); B, *Acmaea digitalis* Eschscholtz, limpet (×0.5).

II, high-tide zone: C, *Littorina scutulata* Gould, periwinkle (×1); D, *Acmaea scabra* (Gould), limpet (×0.5); E, *Balanus glandula* Darwin, acorn barnacle (×0.7); F, *Tegula funebralis* (A. Adams), black turban (×1) claws of *Pagurus* sp., hermit crab protruding; G, *Pachygrapsus crassipes* Randall, common lined shore crab (×0.15).

III, midtide zone: H, *Mytilus californianus* Conrad, California sea mussel (×0.15); I, *Nuttalina californica* (Reeve), California chitin (×0.3); J, *Mopalia muscosa* (Gould), mossy chitin (×0.3); K, *Mitella polymerus* (Sowerby), gooseneck barnacle (×0.25); L, *Balanus tintinnabulum* (Linn.), red and white barnacle (×0.25); M, *Tetraclita squamosa rubescens* Darwin, thatched barnacle (×0.25); N, *Bunodactis elegantissima* (Brandt) (×0.15).

IV, low-tide zone: O, *Anthopleura xanthogrammica* (Brandt), green anemone (×0.15); P, *Spirorbis* sp. (×3); Q, *Strongylocentrotus franciscanus* (A. Agassiz), red sea urchin (×0.35); R, *Astraea undosa* (Wood), top shell (×0.15).

Fig. 3. Rocky shore animals and plants (From Emery, 1960).

In a middle section of the zones of attached organisms at Pacific Grove, California, barnacles and an attached red alga, Endocladia, predominate (Fig. 4). Glynn (1965) defining this zone as a subsystem for purposes of study, considered its structure, food webs, and overall processes. Food available to filter feeders such as the barnacles was estimated by season (Fig. 5). This zone was exposed between 46 and 95% of the time (Fig. 6). The herbivores and carnivores of the rocks were found to move across the zone with the tide, providing energy drains as well as regulatory actions for only part of the tidal cycle (Fig. 7). Total plant tissue (standing crop biomass) representing the balance of photosythesis by the algae and loss to the consumers showed a pulse in the spring when light and nutrient conditions were best. The most active part of the life cycle (Fig. 8) was in the spring, and the nitrogen content per unit of algal tissue was diluted at this season. Photosynthesis occurred in and out of the water but decreased when the plants dried out of water. Based on these and other measurements and experiments a diagram of biomass and food flows for the system was drawn (Fig. 9).

One of the characteristic species at Pacific Grove was a tiny bivalve, Lasaea cistula, which showed continuous reproduction in the rather narrow range of temperature characteristic of the region (Fig. 10), but with a pulse corresponding to the pulse of light (slightly leading the temperature pulse).

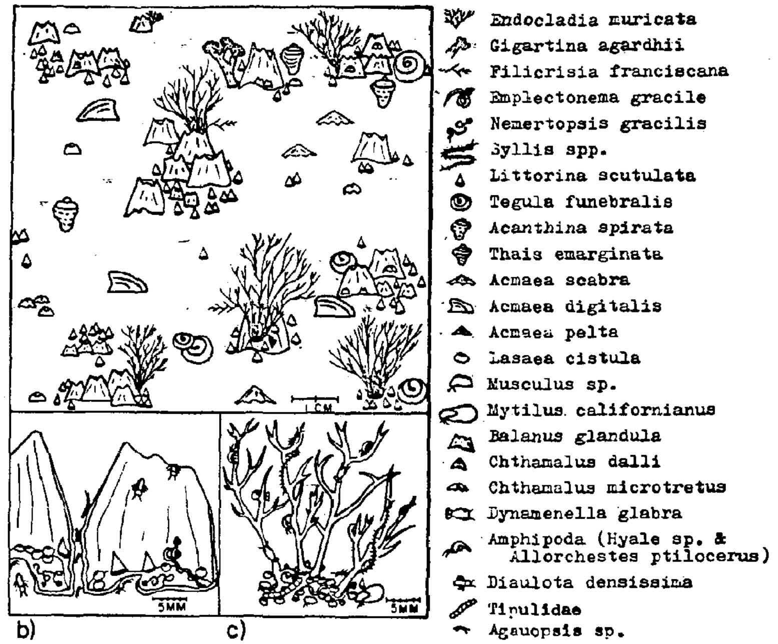
As represented in Fig. 11 from Reish (1968) piling in more sheltered waters, in the shade of wharves, or in turbid inshore waters, may have animal components predominating over algae.

Jetty Rocks of the Gulf Coast

Firm rocky surfaces on the Gulf coast are mainly the man-made rocky jetties, such as those at Port Aransas, and Galveston, Texas, which have a high seasonal range of salinity and temperature. Patterns of zonation according to environmental factors were studied by Whitten, Rosene, and Hedgepeth (1950) and Hedgpeth (1953). The tidal range, the wave amplitude and the seasonal shifts in mean sea level are all of the same order of magnitude: 1 to 4 feet. As shown in Figs. 12 and 13 zones of different organisms are narrow in the inter-tidal region, grading into associations including Arbacia urchins, characteristic of high velocity surface systems (See Chapter A-3). Whereas the green algae at the surface show some increase every spring with increase in light they are kept in check by grazing of the periwinkles and other organisms. The green alga, Ulva, was found to dominate the south jetty at Tuxpan, Mexico in 1958 in waters subjected to freshwater stress and city wastes.

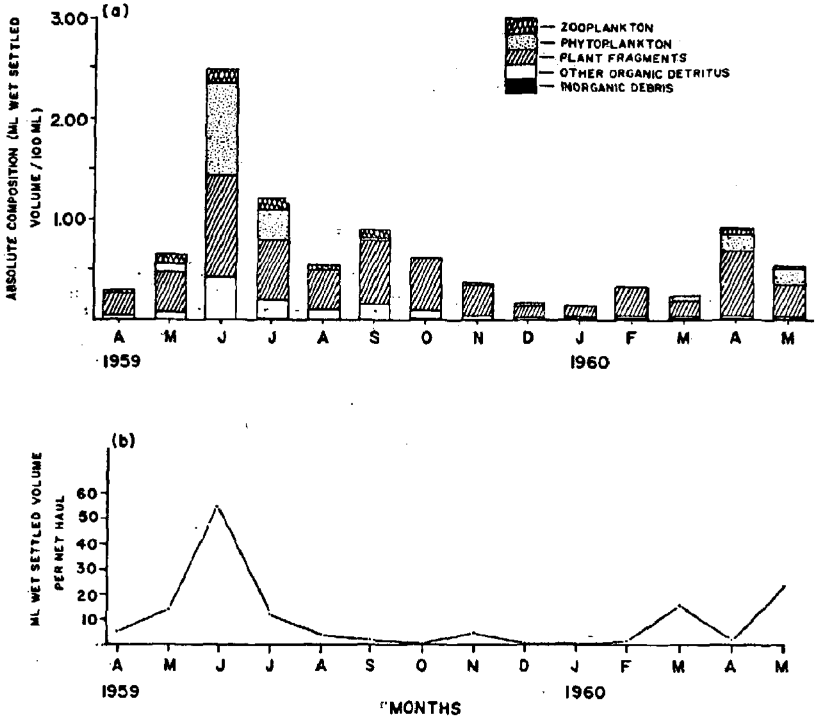
Inter-tidal Algal and Mussel Beds of Maine

As one moves northward on the Atlantic coast, geological formations in Massachusetts shift from sand to rock and tidal ranges increase from 10 to 20 feet or more. Exposed in varying degrees, the much dissected coast of


Endocladia muricata
Gigartina agardhii
Filicrisia franciscana
Emplectonema gracile
Nemertopsis gracilis
Syllis spp.
Littorina scutulata
Tegula funebralis
Acanthina spirata
Thais emarginata
Acmaea scabra
Acmaea digitalis
Acmaea pelta
Lasaea cistula
Musculus sp.
Mytilus californianus
Balanus glandula
Chthamalus dalli
Chthamalus microtretus
Dynamenella glabra
Amphipoda (Hyale sp. & Allorchestes ptilocerus)
Diaulota densissima
Tipulidae
Agauopsis sp.
1 CM
5MM
5MM
b)
c)

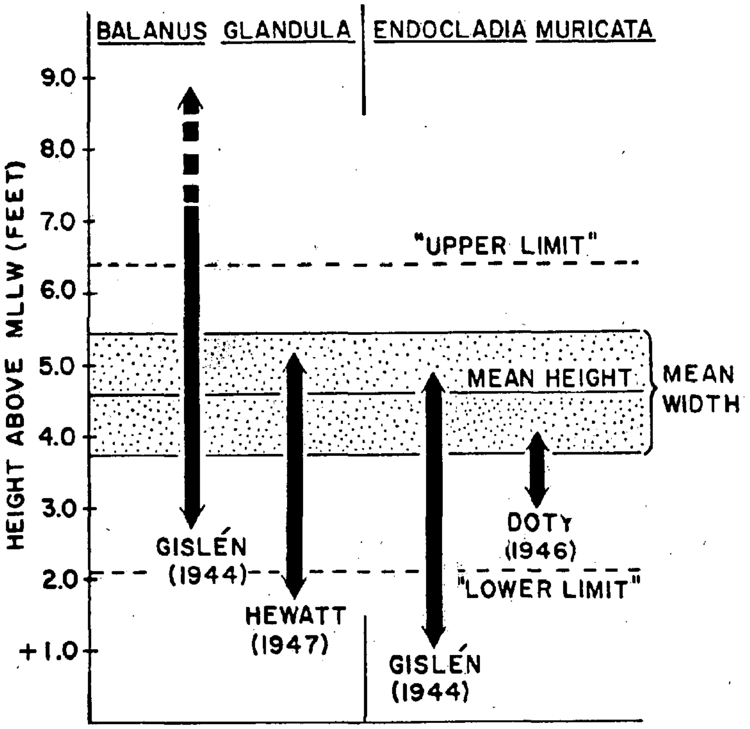
Spatial arrangement of some of the more common benthic species in the *Endocladia-Balanus* association. The quantities of organisms represented in fig. 69-a are proportional to those tallied in Quadrat VI. Fig. 69-b shows a magnified view of portions of the interiors of two empty shells of *B. glandula*. Fig. 69-c. shows an enlarged portion of the thallus of *E. muricata*.

Fig. 4. Barnacle-algal zone in California (From Glynn 1965).



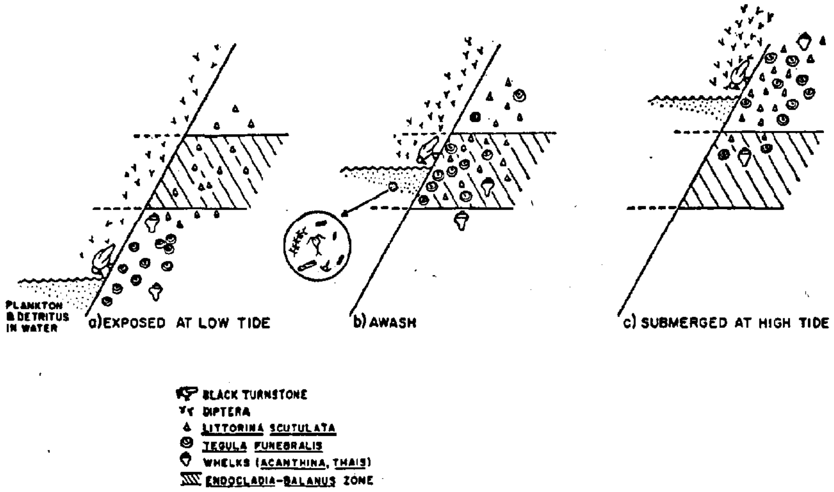
(a) Monthly averages of relative and absolute amounts of each material taken in the *Endocladia-Balanus* association at high water over the period, April, 1959-May, 1960. (b) Monthly averages of wet settled volume of phytoplankton captured per haul at bell buoy in southern Monterey Bay, approximately 1,000 yards offshore of the *Endocladia-Balanus* study area. Based on vertical hauls, 15 meters to surface, made weekly, using a truncated Apstein net ¼ meter in greatest diameter, mouth ring 18 cm in diameter, and filtering surface of # 20 bolting silk. Data collected by Hopkins Marine Station personnel as part of the California Cooperative Oceanic Fisheries Investigations program.

Fig. 5. Regimes of food available to the barnacle algal zone (Glynn, 1965).



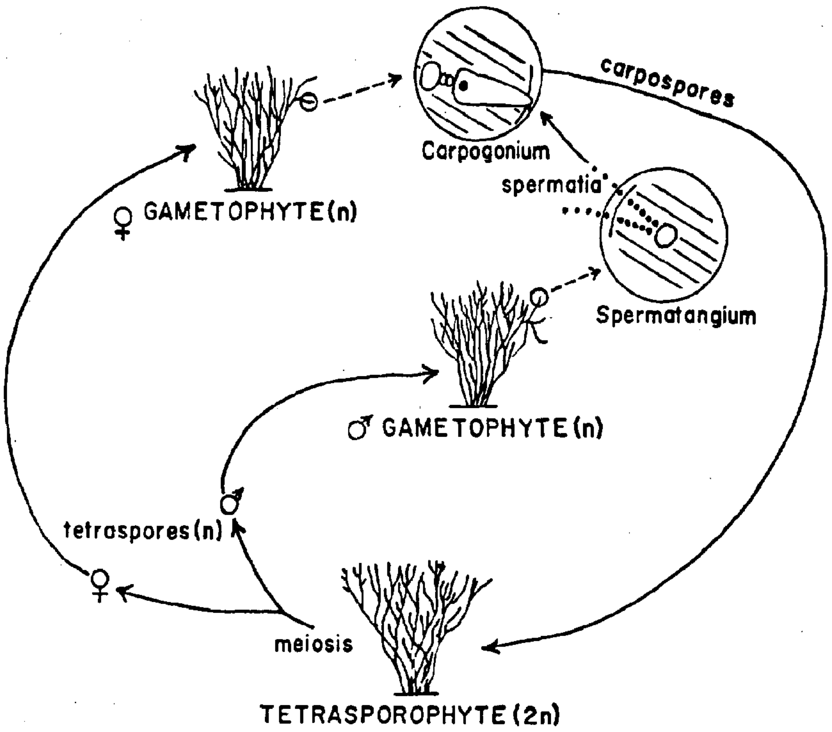
Comparison of the vertical ranges of *B. glandula* and *E. muricata* at the Hopkins Marine Station as established by various workers, with the vertical position of the 16 quadrats collected from the *Endocladia-Balanus* association. Upper and lower limits represent the over-all vertical range of the *Endocladia-Balanus* association in the vicinity of the quadrat sites.

Fig. 6. Tidal relations of the barnacle-algal zone (Glynn, 1965).


PLANKTON & DETRITUS IN WATER
a) EXPOSED AT LOW TIDE
b) AWASH
c) SUBMERGED AT HIGH TIDE
BLACK TURNSTONE
DIPTERA
LITTORINA SCUTULATA
TEGULA FUNEBRALIS
WHELKS (ACANTHINA, THAIS)
ENDOCLADIA-BALANUS ZONE

Movement of some transient species into, through, and above the *Endo-ladia-Balanus* level during a rising tide.

Fig. 7. Movements of some carnivores with rising tide (Glynn, 1965).

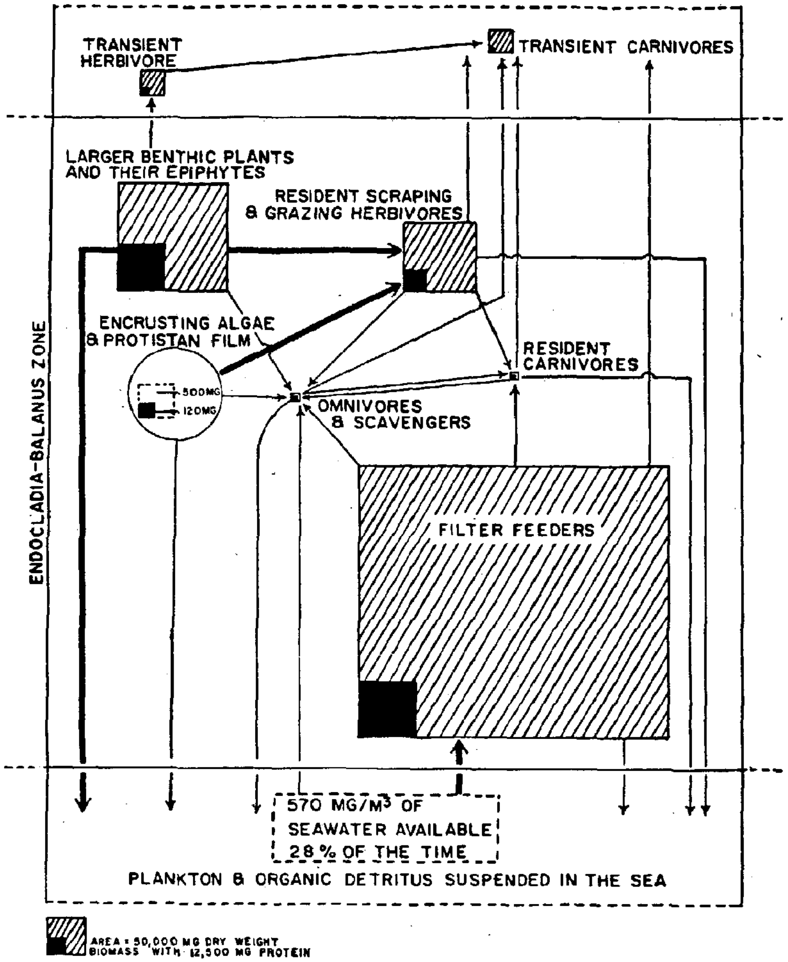

carpospores
Carpogonium
spermatia
Spermatangium
♀ GAMETOPHYTE(n)
♂ GAMETOPHYTE(n)
♂
tetraspores(n)
♀
meiosis
TETRASPOROPHYTE(2n)

Major events in the life cycle of *E. muricata*, as adapted from KYLIN (1928).

Seasonal variation of *E. muricata* (dry weight) for study areas I, II, and III. Each monthly figure represents combined data from three field samples.

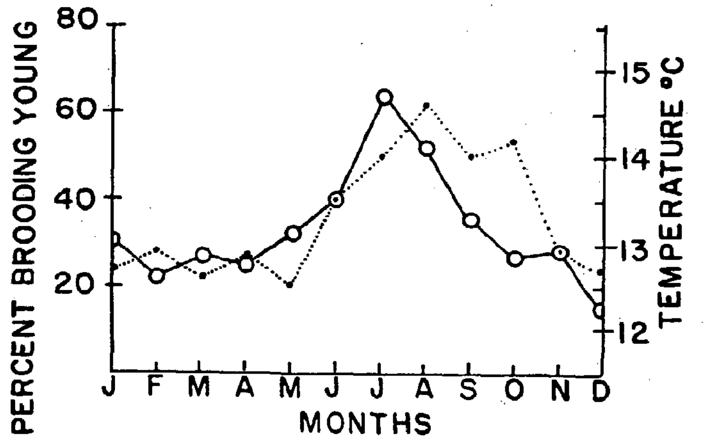
Month		Standing crop biomass		
		g/ 2,034 cm²	g/m²	Seasonal average g/m²
April,	1959	44.9	221	SPRING 189
May,	„	35.7	176	
June,	„	34.8	171	
July,	„	31.0	152	SUMMER 128
Aug.,	„	29.7	146	
Sept.,	„	17.4	85	
Oct.,	„	25.9	127	AUTUMN 87
Nov.,	„	19.0	93	
Dec.,	„	8.3	41	
Jan.,	1960	24.0	118	WINTER 79
Feb.	„	12.6	62	
Mar.,	„	11.7	58	

Fig. 8. Reproductive cycle and seasonal record of growth of red algal dominant in barnacle-algal zone (Glynn, 1965).


TRANSIENT HERBIVORE
TRANSIENT CARNIVORES
LARGER BENTHIC PLANTS AND THEIR EPIPHYTES
RESIDENT SCRAPING & GRAZING HERBIVORES
ENCRUSTING ALGAE & PROTISTAN FILM
500MG
120MG
RESIDENT CARNIVORES
OMNIVORES & SCAVENGERS
FILTER FEEDERS
ENDOCLADIA-BALANUS ZONE
570 MG/M³ OF SEAWATER AVAILABLE 28 % OF THE TIME
PLANKTON & ORGANIC DETRITUS SUSPENDED IN THE SEA
AREA = 50,000 MG DRY WEIGHT BIOMASS WITH 12,500 MG PROTEIN

Block diagrams showing average dry weight biomass and protein content of the organisms of the *Endocladia-Balanus* association, grouped in categories according to food relations. The area of the shaded and solid block for each group is proportional to its dry weight biomass and protein content per m² (see key, lower left-hand corner). Arrows show the main pathways in flow of food. Unknown quantities of certain groups are delineated by broken lines, and for the encrusting algae and protistan film an estimate of the very small quantities present is shown in a magnified view.

Fig. 9. Energy diagram for the barnacle-algal zone (Glynn, 1965).



Three year monthly means of the percent of adult *L. cistula* brooding young (solid line), and inshore sea water temperatures at Pacific Grove, California (broken line), for the years 1959—1961.

Fig. 10. Reproductive activity of a small snail member of the barnacle-algal association

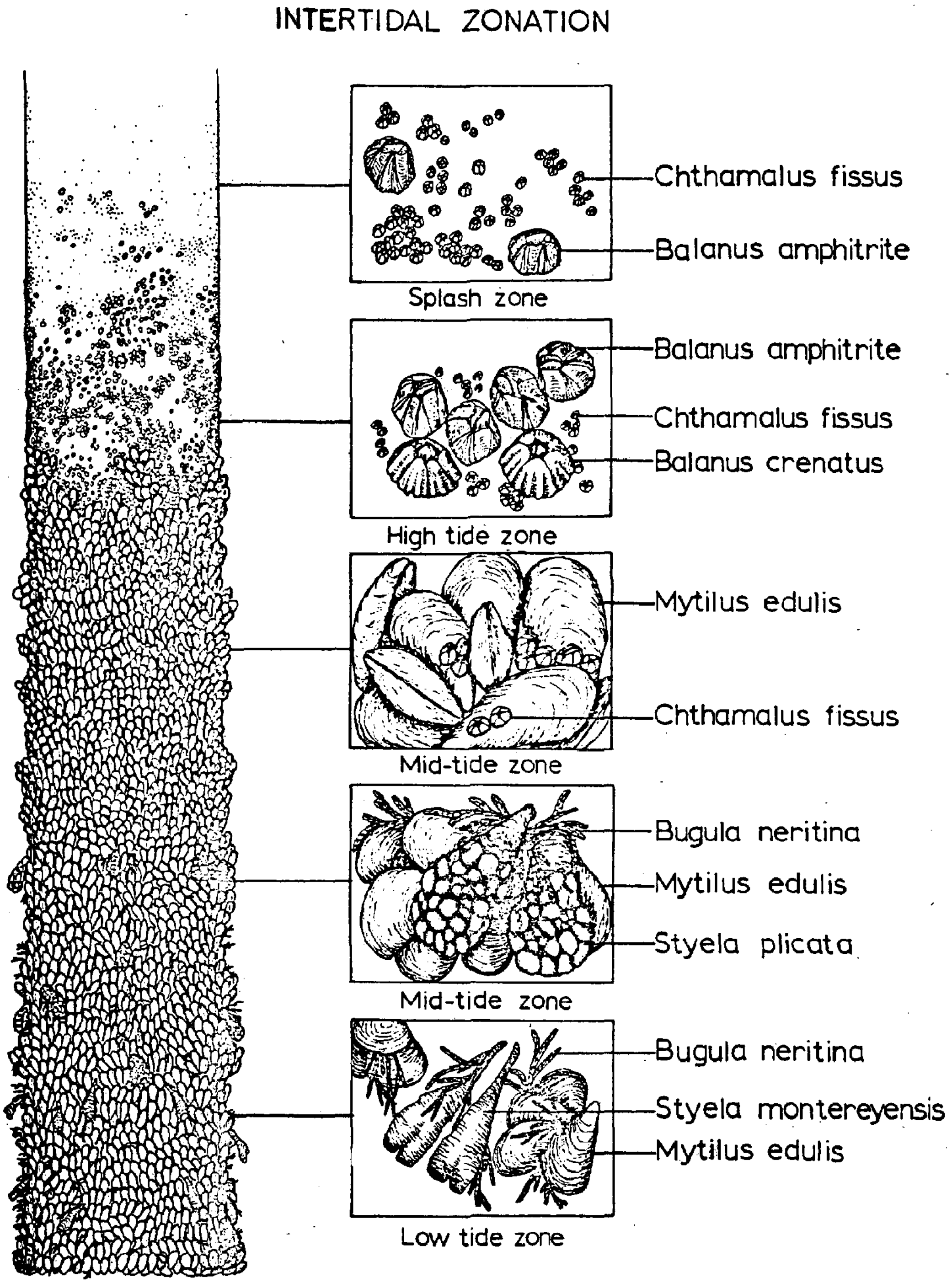
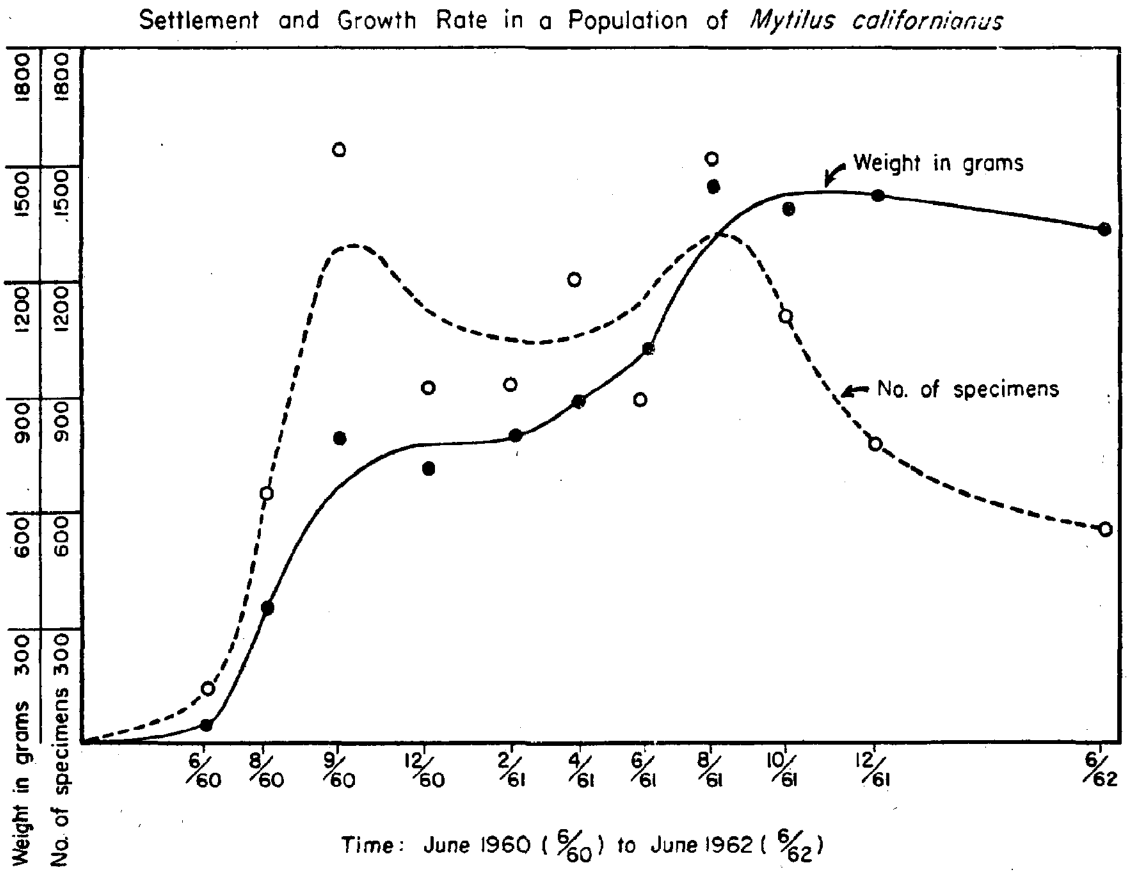

INTERTIDAL ZONATION
Chthamalus fissus
Balanus amphitrite
Splash zone
Balanus amphitrite
Chthamalus fissus
Balanus crenatus
High tide zone
Mytilus edulis
Chthamalus fissus
Mid-tide zone
Bugula neritina
Mytilus edulis
Styela plicata
Mid-tide zone
Bugula neritina
Styela montereyensis
Mytilus edulis
Low tide zone

Fig. 11 A. Intertidal zonation in Alamitos Bay (From Reish, 1968).



Graph showing settlement and growth rate of a population of *Mytilus californianus* in Ventura County Marina, California

Fig. 11B. Succession on a California jetty (Reish, 1964a).

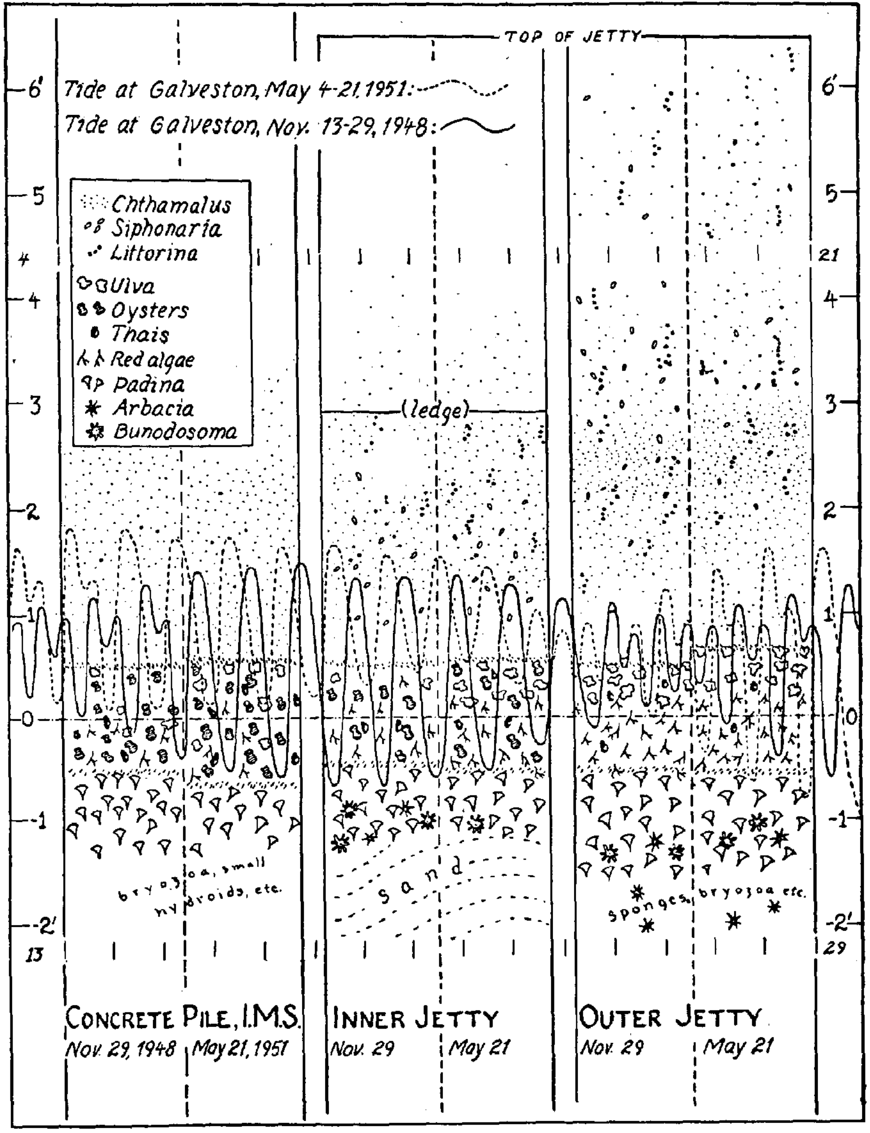
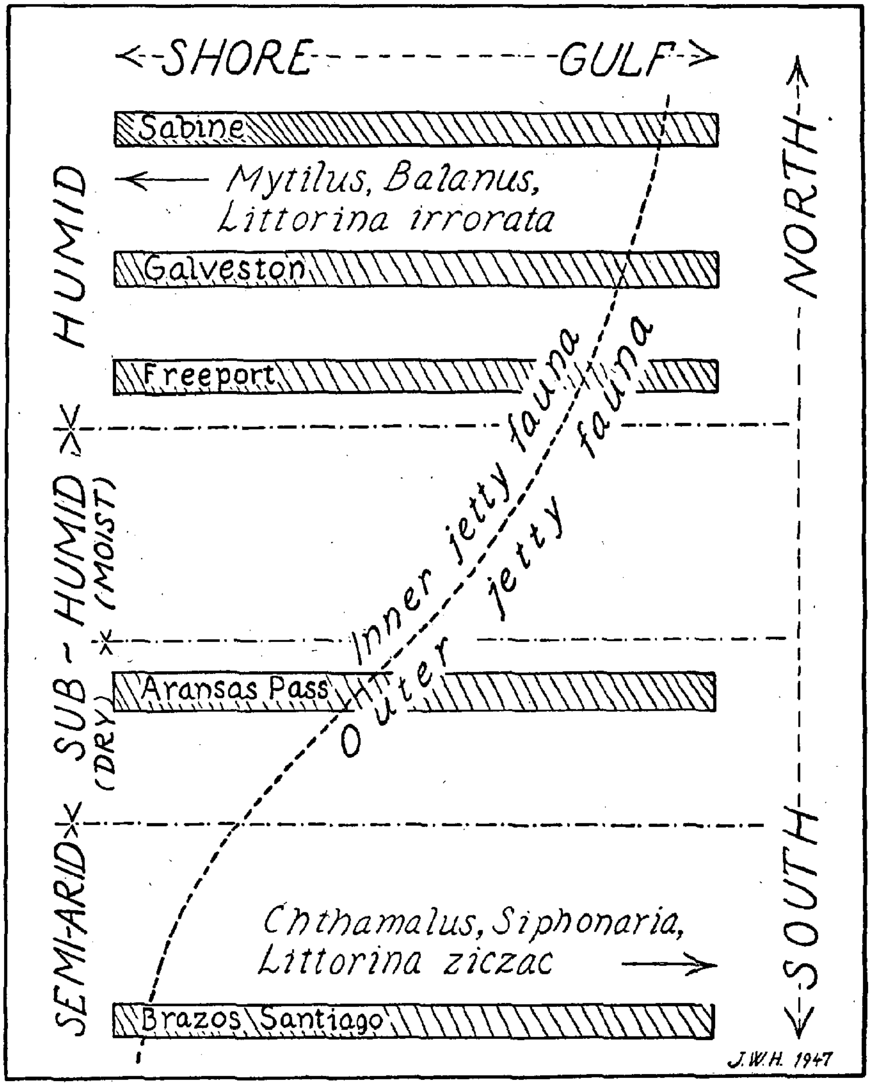

TOP OF JETTY
Tide at Galveston, May 4-21, 1951:
Tide at Galveston, Nov. 13-29, 1948:
Chthamalus
Siphonaria
Littorina
Ulva
Oysters
Thais
Red algae
Padina
Arbacia
Bunodosoma
(ledge)
bryozoa, small hydroids, etc.
sand
sponges, bryozoa etc.
6'
5
4
3
2
1
0
-1
-2'
21
13
29
CONCRETE PILE, I.M.S.
Nov. 29, 1948
May 21, 1951
INNER JETTY
Nov. 29
May 21
OUTER JETTY
Nov. 29
May 21

Diagram representing zonation on concrete piling and jetties at Port Aransas, as observed on November 29, 1948, and May 21, 1951, with the predicted tide curves for the two-week period preceding observations superimposed.

Fig. 12. Zonation in western Gulf of Mexico where tidal range is small (From Hedgepeth 1953).


SHORE
GULF
Sabine
Mytilus, Balanus,
Littorina irrorata
Galveston
Freeport
HUMID
SUB - HUMID (MOIST)
SUB - HUMID (DRY)
SEMI-ARID
inner jetty fauna
outer jetty fauna
Aransas Pass
Chthamalus, Siphonaria,
Littorina ziczac
Brazos Santiago
NORTH
SOUTH
J.W.H. 1947

Schematic diagram of relationships of intertidal jetty fauna with climatic zones and latitude. Characteristic members of the fauna are indicated.

Fig. 13. Comparison of intertidal zonation in the western gulf. Northern jetties receive large variations in salinity, whereas those further south have higher and more stable salinities (Whitten, Rosene, and Hedgepeth, 1950).

Maine with its inlets and archipelagoes, has a large representation of the intertidal rocky ecosystem made up of heavy beds of brown algae, beds of mussels, and such carnivores as starfishes, green crabs, and lobsters that move into the system when it is inundated. The mussels filter the products of plankton systems from the water and regenerate nutrients among the algal beds which, after photosynthetic growth, return organic matter to the plankton systems bathing the rocks. Chapman (1964) provides diagrams from Lewis of similar beds in England (Figs. 14 and 15). Chlorophyll a content of the various layers is given in Tables 1 and 2 from Gifford and E. P. Odum (1961).

Tropical Atlantic Intertidal Rocks

On Margarita Island, Venezuela (Fig. 16) zonation is presented by Rodriquez (1959) as shown in Figures 17-19 and 21. Here salinities are high and vary little. Whereas ecosystems under water were found to be tropical, diversified, and very different from those in temperate latitudes, intertidal zonation was similar to that of temperate regions having few species at a time and with periwinkle, barnacle, red algae and urchin zones. Some niche substitutions were observed. In Fig. 18 the stressed outer zones were characterized by the green alga Ulva, whereas the less exposed surfaces had other algae. Zonation data for ~~tropical~~ Africa are given in Figs. 32, 34, and 35.

Tropical Pacific Intertidal Rocks

Doty provides information on zonation on intertidal rocks in Hawaii (Fig. 20). Similar data are given for the West Coast in Figs. 29 and 30.

Examples of Intertidal Surfaces Affected by Wastes

The green alga Ulva may be characteristic of harbors that are heavily affected with wastes such as sewage that constitute a fertilization as well as a stress in oxygen variability and other properties. When Eniwetok Lagoon was receiving heavy shipping Ulva and Enteromorpha developed on intertidal surfaces. These algae were also prevalent in waste-laden San Juan Harbor in 1963, and McNulty, Reynolds, and Miller (1960) reported their distribution on rocks and posts in the vicinity of the sewage outfall into Biscayne Bay near Miami, Florida (See Figs 22 and 23).

The encrusting, attached ecological systems of the rocky sea fronts form a steady state, with algae continually growing and being grazed back. The system has considerable ability to groom, clean, and mineralize substances that tend to be deposited on the rocky surfaces. For example, Ceramé-Vivas (1968a) reports that rocks around San Juan, Puerto Rico experienced fairly rapid return to normal after a large oil spill there.

DISCUSSION

Exposed versus Sheltered Sea Fronts

Sea front ecosystems receiving heavy wave action with spray undergo some energy draining destructive action but may be better protected from intertidal heating and drying than those of quieter coasts. Several authors

Tables 1 and 2. Chlorophyll in intertidal algal zones of New England (Gifford and Odum, 1961).

TABLE 1. *Average chlorophyll* a *in four zones in the intertidal region.*

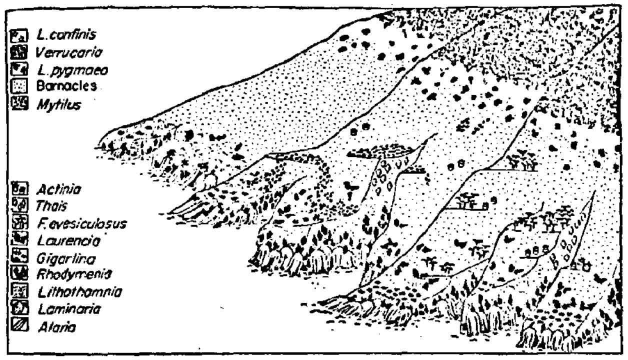
Zones	No. of samples	Mean (g/m²)	Standard deviation
1. "Black" (100% coverage)*	25	0.80 ± .009	0.48
"Black" (63% coverage)*	25	0.50	
2. Barnacle (100% coverage)	52	0.27 ± .001	0.19
3. *Fucus-Balanus* (100% coverage)	50	1.47 ± .051	0.86
4. "Seaweed" (100 % coverage)	50	1.04 ± .009	0.68
Mean of all zones	175	0.82	.52

* Two values are given for "black" zone—one is the concentration within the patches of algae and the other value is average concentration for the zone as a whole (which is not completely covered by plants).

TABLE 2. *Inter-zone comparison of chlorophyll content in grams per square meter*

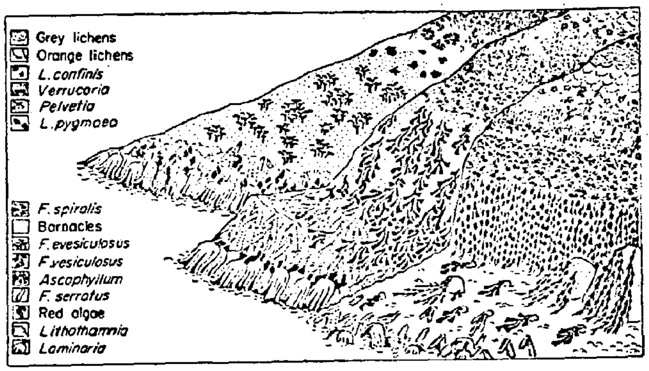
Zones compared*	difference	S.E. of differences	t	P
1 vs. 2	.23	.03	7.4	>.01
1 vs. 3	.87	.12	7.2	>.01
1 vs. 4	.54	.14	3.9	>.01
2 vs. 3	1.19	.13	9.6	>.01
2 vs. 4	.76	.03	24.6	>.01
3 vs. 4	.43	.16	2.8	>.01

* See Table 1 for names of zones.

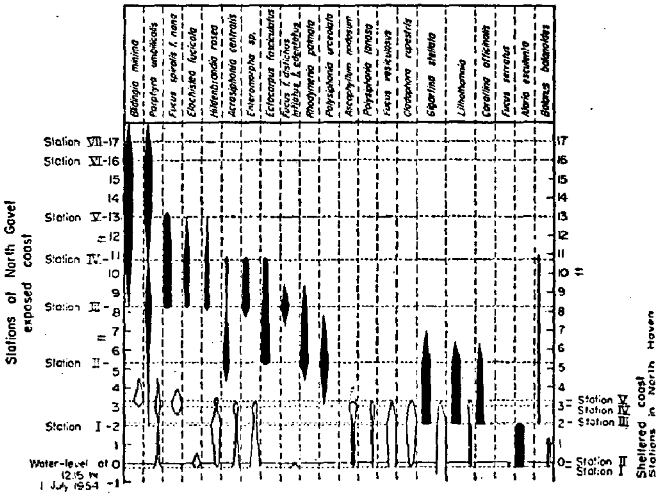

L. confinis
Verrucaria
L. pygmaea
Barnacles
Mytilus
Actinia
Thais
F. evesiculosus
Laurencia
Gigartina
Rhodymenia
Lithothamnia
Laminaria
Alaria

Diagrammatic representation of types of exposed shores around Anglesey. The slope on the left represents a simple extremely exposed shore with few species superimposed upon the barnacles. The other slopes show slightly less exposed shores and indicate the influence of ledges and clefts upon the distribution of Mytilus, Fucus *var.* evesiculosus *and* Thais. *Although shown separately* Mytilus *and* Fucus *often occur together. The depth of the black zone has been considerably reduced: on these shores it would probably be at least twice as deep as the barnacle zone. Note that* Patella, Littorina neritoides, L. rudis *and* Porphyra *would also be abundant but are not shown (after Lewis).*

Fig. 14. Atlantic intertidal zonation (Chapman, 1964).

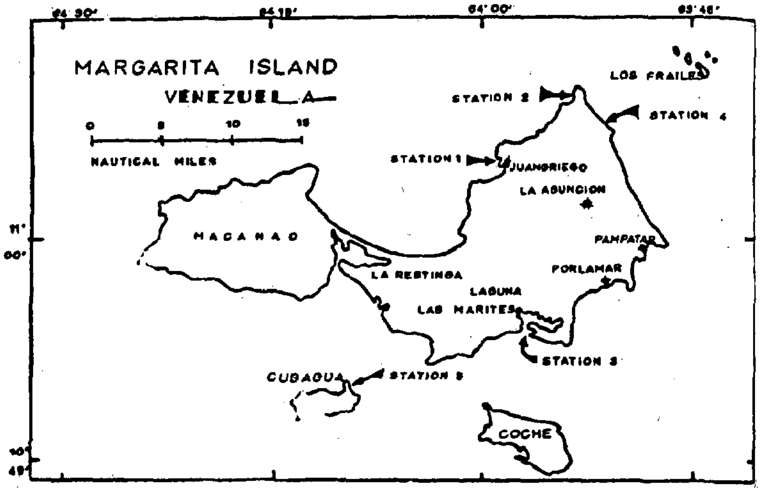

Grey lichens
Orange lichens
L. confinis
Verrucaria
Pelvetia
L. pygmaea
F. spiralis
Barnacles
F. evesiculosus
F. vesiculosus
Ascophyllum
F. serratus
Red algae
Lithothamnia
Laminaria

Diagrammatic representation of one semi-exposed and two sheltered shores around Anglesey, wave action decreasing from left to right. On the sheltered shores the influence of slope and substratum upon the large algae is shown. No attempt has been made to include animals other than barnacles (after Lewis).



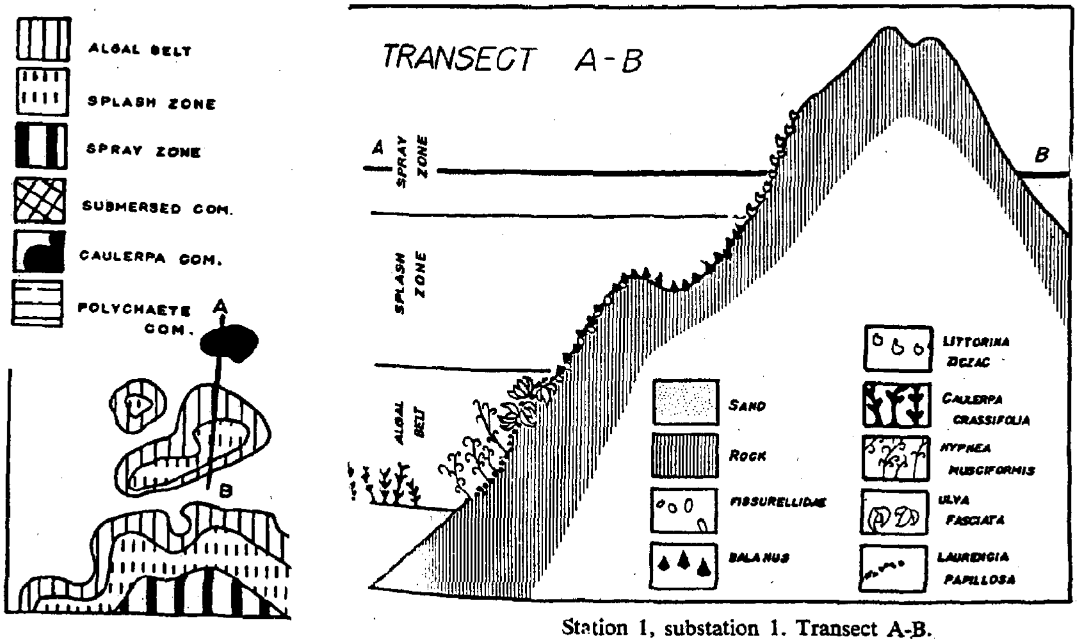
Comparison of the distribution of inter-tidal algae in relation to tide levels. Fair Isle, June–July 1952. Dark bands for exposed coast, plain for sheltered coast (after Burrows et al.).

Fig. 15. Algal zonation in the North Atlantic zonation (Chapman, 1964).


MARGARITA ISLAND
VENEZUELA
0 5 10 15
NAUTICAL MILES
64°30'
64°15'
64°00'
63°45'
11°
00'
10°
45'
LOS FRAILES
STATION 2
STATION 4
STATION 1
JUANGRIEGO
LA ASUNCION
MACANAO
PAMPATAR
PORLAMAR
LA RESTINGA
LAGUNA
LAS MARITES
STATION 3
CUBAGUA
STATION 5
COCHE

Map of Margarita Island, showing position of stations.

Fig. 16. Location of Tropical Zonation studies by Rodriquz (1959) on North Shore of Venezuela.

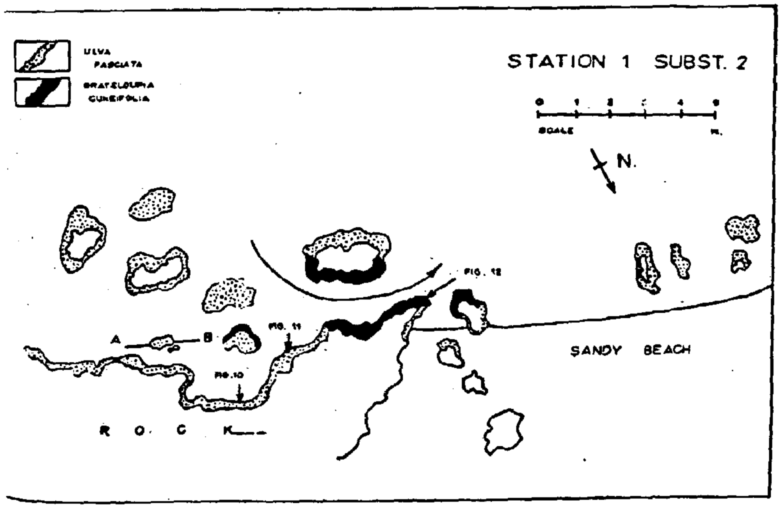

ALGAL BELT
SPLASH ZONE
SPRAY ZONE
SUBMERSED COM.
CAULERPA COM.
POLYCHAETE COM.
A
B
TRANSECT A-B
A
SPRAY ZONE
B
SPLASH ZONE
ALGAL BELT
SAND
ROCK
FISSURELLIDAE
BALANUS
LITTORINA ZICZAC
CAULERPA CRASSIFOLIA
HYPNEA MUSCIFORMIS
ULVA FASCIATA
LAURENCIA PAPILLOSA

Station 1, substation 1. Transect A-B.

Fig. 17. Transect of intertidal zonation on Margarita Island facing the sea.

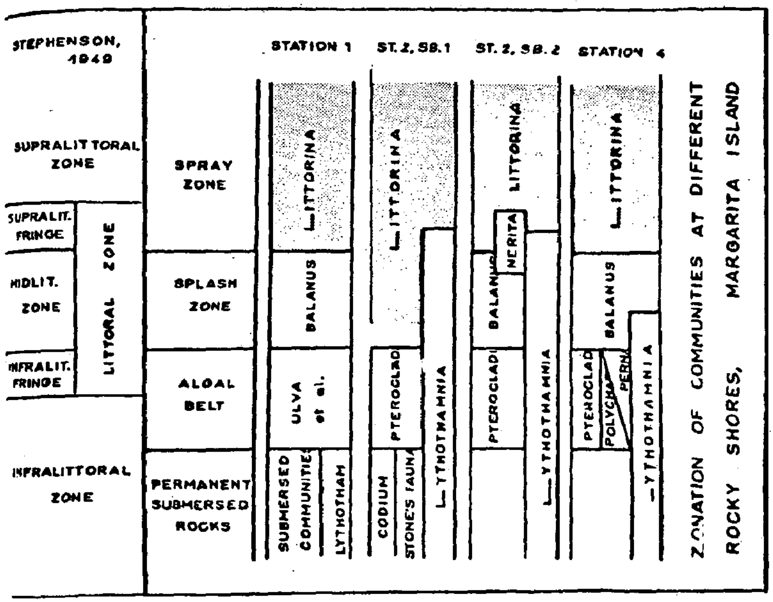
COMPARATIVE TEMPERATURES OF AIR, POLYCHAETE POOL AND *Halichondria* COMMUNITY OF STATION 1, SUBST. 1, AUGUST 19, 1956. (° C.)

Time	*Air*	*Halich. Comm.*	*Polych. Pool.*
8.15	27.5	26.2	26.5
9.15	26.0	26.2	26.5
10.15	31.0	27.0	28.2
11.15	30.5	27.7	28.5
12.15	31.5	27.3	27.5
13.15	32.0	27.3	27.5
14.15	30.5	26.8	26.8
15.15	27.0	26.2	26.0
16.15	27.5	25.9	25.8
17.15	25.0	25.5	25.2


ULVA FASCIATA
GRATELOUPIA CUNEIFOLIA
STATION 1 SUBST. 2
0 1 2 3 4 5
SCALE
M.
N.
FIG. 12
FIG. 11
FIG. 10
A
B
SANDY BEACH
R O C K

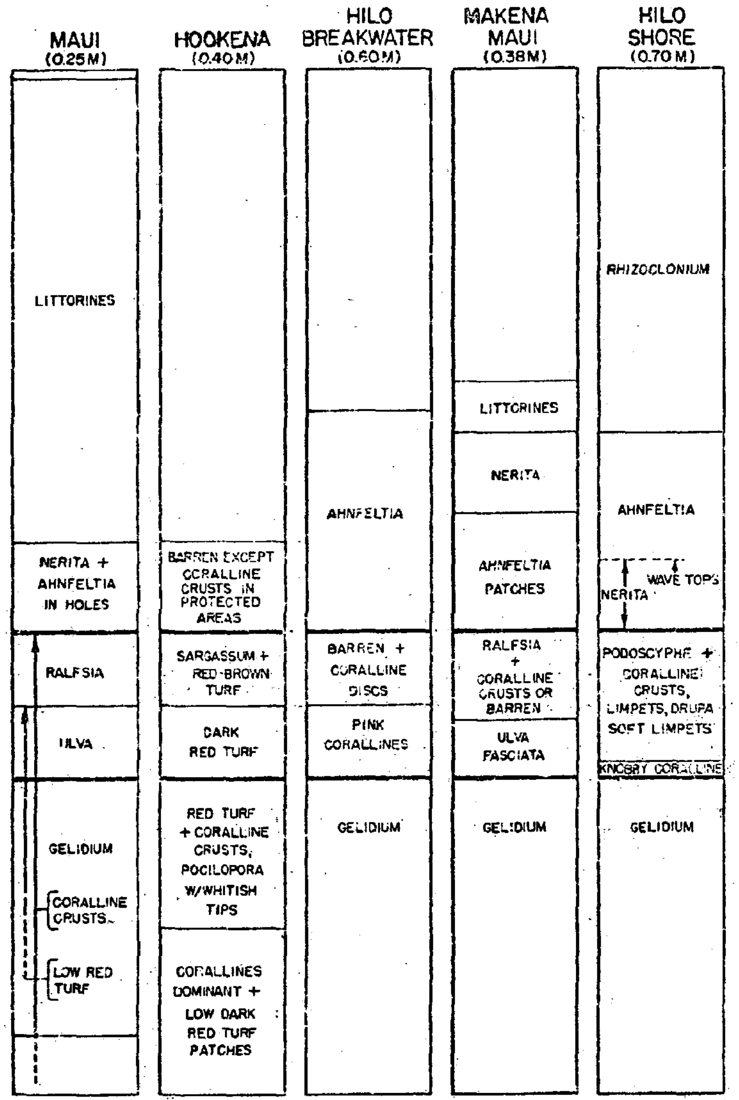
Station 1, substation 2. General map showing substitution of *Ulva*.

Fig. 18. Ulva domination of a tropical intertidal zone (Rodriquez, 1959).


STEPHENSON, 1949
SUPRALITTORAL ZONE
SUPRALIT. FRINGE
MIDLIT. ZONE
INFRALIT. FRINGE
LITTORAL ZONE
INFRALITTORAL ZONE
SPRAY ZONE
SPLASH ZONE
ALGAL BELT
PERMANENT SUBMERSED ROCKS
STATION 1
ST. 2, SB. 1
ST. 2, SB. 2
STATION 4
LITTORINA
BALANUS
ULVA et al.
SUBMERSED COMMUNITIES
LYTHOTHAM
PTEROCLAD
CODIUM
STONE'S FAUNA
LYTHOTHAMNIA
NERITA
POLYCHA
PERN
ZONATION OF COMMUNITIES AT DIFFERENT ROCKY SHORES, MARGARITA ISLAND

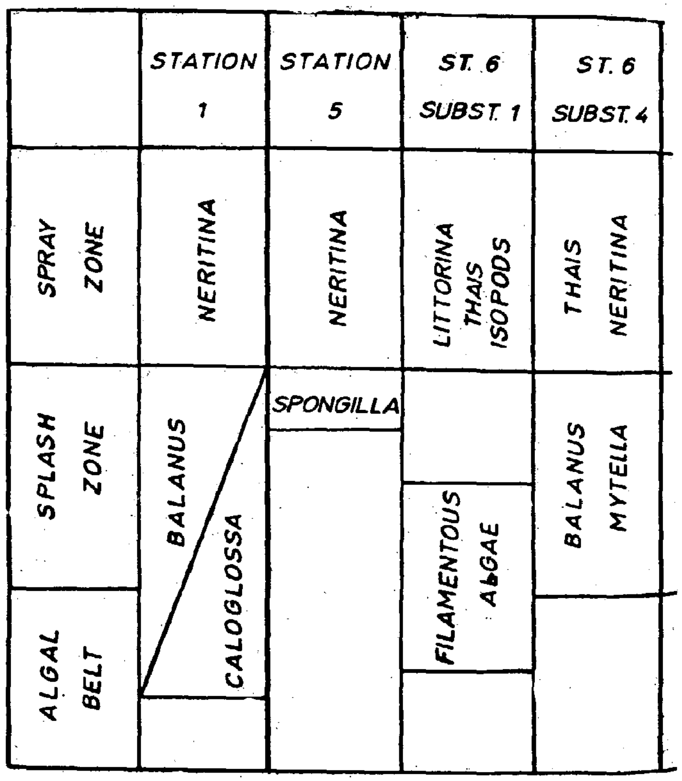
General scheme of the rocky shores.

Fig. 19. Zonation of Margarita Island, Venezuela, (From Rodriquez 1959).


MAUI (0.25M)
HOOKENA (0.40M)
HILO BREAKWATER (0.60M)
MAKENA MAUI (0.38M)
HILO SHORE (0.70M)
LITTORINES
NERITA + AHNFELTIA IN HOLES
RALFSIA
ULVA
GELIDIUM
CORALLINE CRUSTS
LOW RED TURF
BARREN EXCEPT CORALLINE CRUSTS IN PROTECTED AREAS
SARGASSUM + RED-BROWN TURF
DARK RED TURF
RED TURF + CORALLINE CRUSTS, POCILOPORA W/WHITISH TIPS
CORALLINES DOMINANT + LOW DARK RED TURF PATCHES
AHNFELTIA
BARREN + CORALLINE DISCS
PINK CORALLINES
GELIDIUM
LITTORINES
NERITA
AHNFELTIA PATCHES
RALFSIA + CORALLINE CRUSTS OR BARREN
ULVA FASCIATA
GELIDIUM
RHIZOCLONIUM
AHNFELTIA
WAVE TOPS
NERITA
PODOSCYPHE + CORALLINE CRUSTS, LIMPETS, DRUPA SOFT LIMPETS
KNOBBY CORALLINE
GELIDIUM

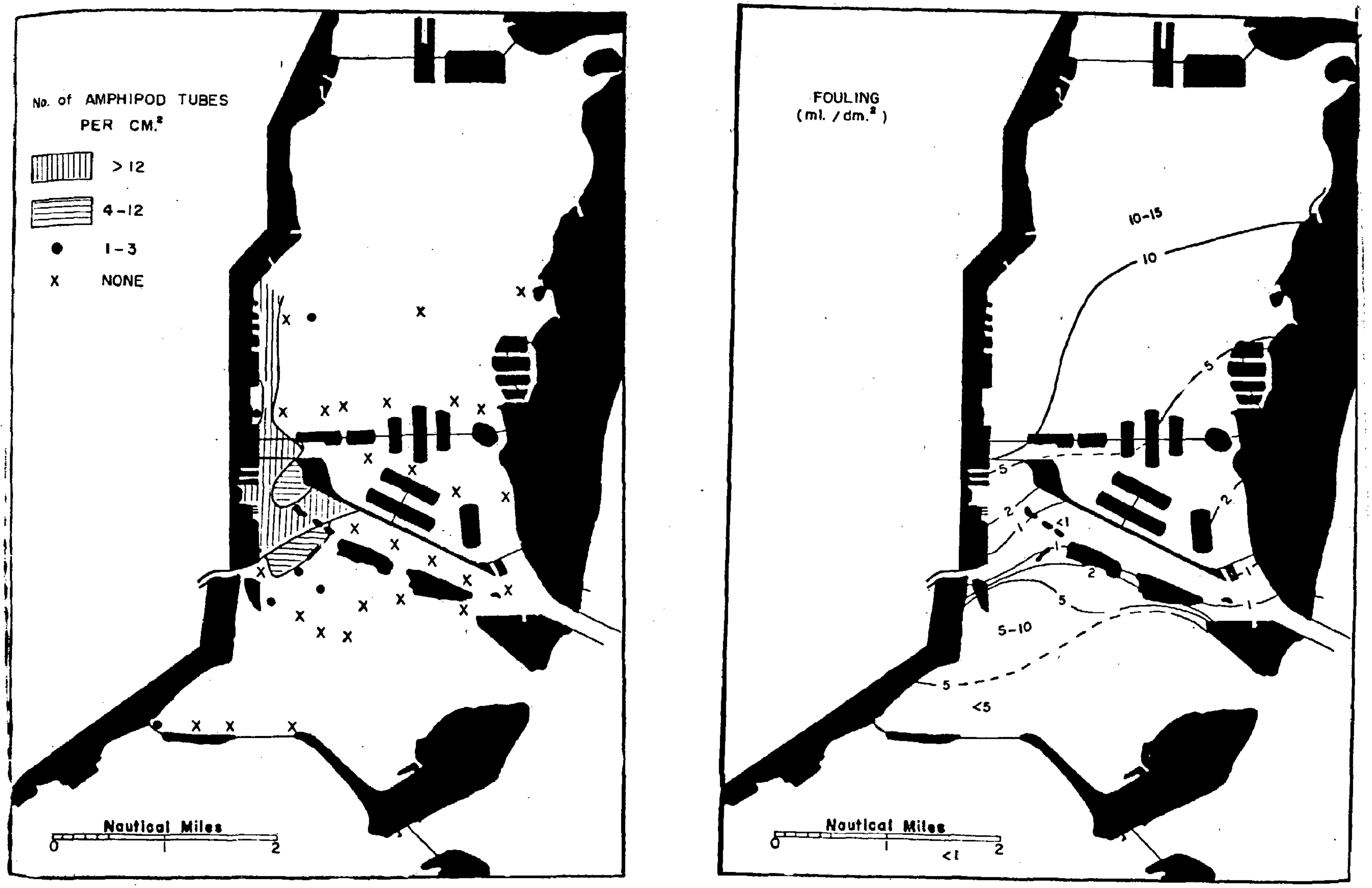
The vertical distribution patterns common to mature Hawaiian shore areas for three places on the island of Hawaii and two places on the nearby island of Maui. The distance in meters given at the top of each strip is the distance between the two horizontal dark lines across it and, thus, provides a scale for that strip. The necessity for different scales in this area where the tidal phenomena are relatively uniform is correlated with differing degrees of wave action.

Fig. 20. Intertidal zonation in Hawaii (Doty,1967o).


STATION 1
STATION 5
ST. 6 SUBST. 1
ST. 6 SUBST. 4
SPRAY ZONE
SPLASH ZONE
ALGAL BELT
NERITINA
BALANUS
CALOGLOSSA
NERITINA
SPONGILLA
LITTORINA THAIS ISOPODS
FILAMENTOUS ALGAE
THAIS NERITINA
BALANUS MYTELLA

General scheme of zonation on hard substratum.

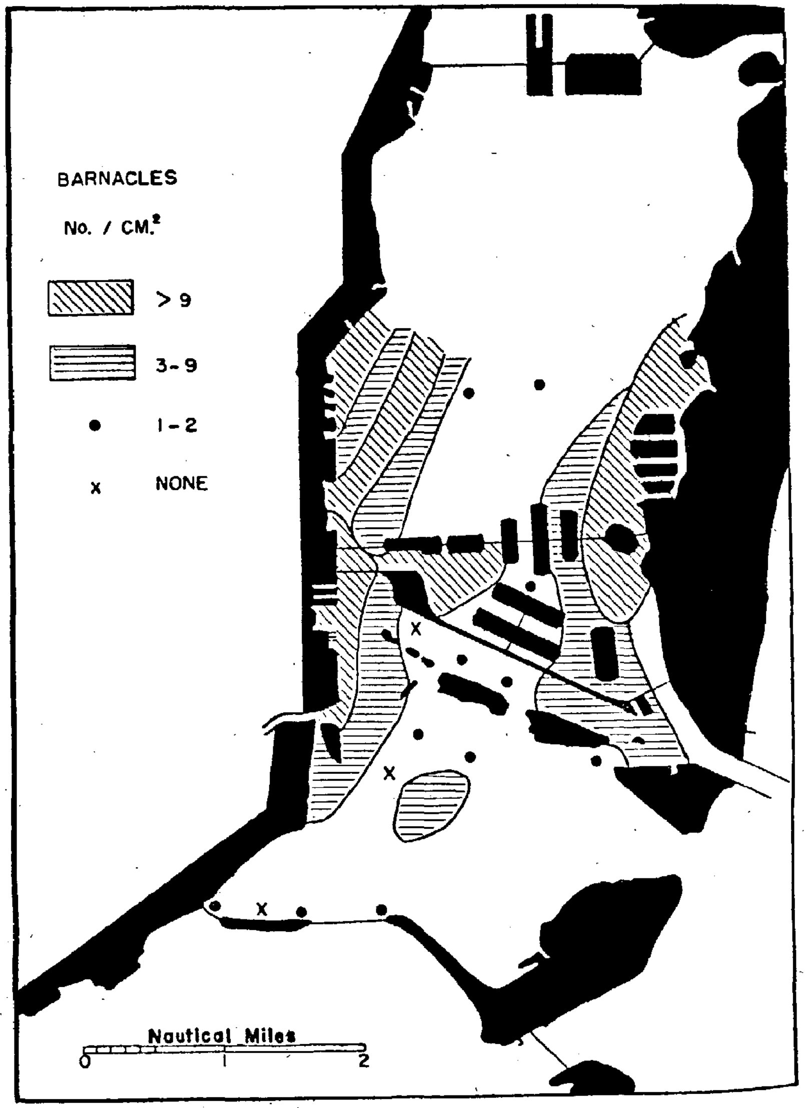
Fig. 21. Intertidal zonation under stress of salinity variation in a tropical situation, Lake Maracaibo, Venezuela (Rodriguez, 1963).


No. of AMPHIPOD TUBES PER CM.^{2}
> 12
4-12
1-3
NONE
Nautical Miles
0
1
2
FOULING (ml. / dm.^{2})
10-15
10
5
2
1
<1
5-10
<5
Nautical Miles
0
1
<1
2

Horizontal distribution of amphipod tubes, stake experiment.

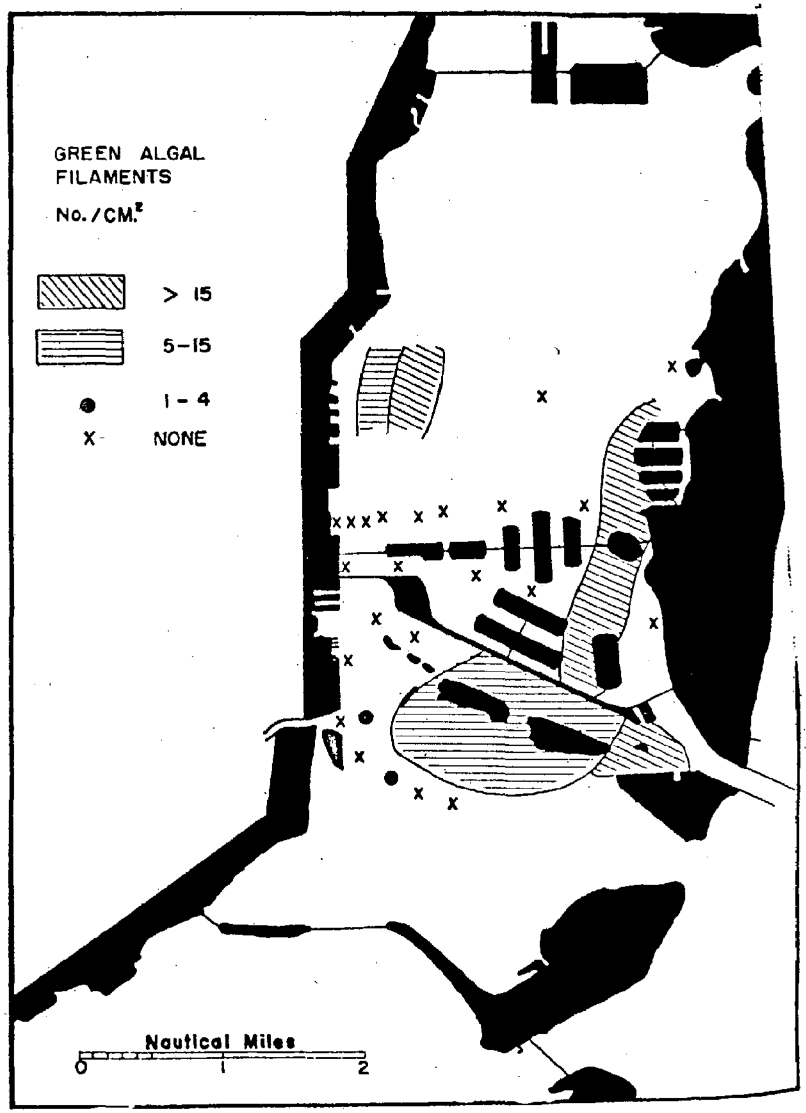
Horizontal distribution of mean displacement volumes of fouling organisms, glass panel experiments.

Fig. 22. Tube building crustacea and encrusting organisms in vicinity of waste outfalls in Biscayne Bay Miami (McNulty, 1961).


BARNACLES
No. / CM.^{2}
> 9
3-9
1-2
NONE
Nautical Miles
0
1
2

Horizontal distribution of barnacles, stake experiment.

Fig. 23. Tube building crustacea and encrusting organisms in vicinity of waste outfalls in Biscayne Bay, Miami from McNulty (1961).


GREEN ALGAL
FILAMENTS
No./CM.^{2}
> 15
5-15
1 - 4
NONE
Nautical Miles
0
1
2

Horizontal distribution of green algal filaments, stake experiment.

Ulva, *Enteropmorpha* and *Cladophora* in Biscayne Bay, Miami Fla. (From McNulty 1961).

have diagrammed the change in zonation from exposed sea front to sheltered sea front as a narrowing of life zones occupied by populations. Niche substitutions and/or species elimination occur in the change from one regime to the other (See examples in Figs. 12, and 24-26).

Vertical Zonation

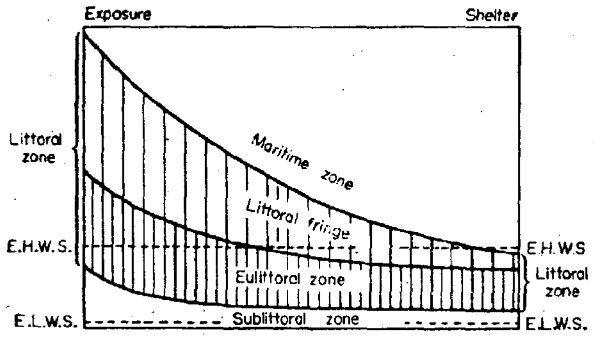
Many authors have diagrammed vertical zonation relative to the levels of the tide, such as mean sea level, high spring tide, splash zone, etc. In different areas the species occupying the various tidal zones are different due to niche substitution, the complicating action of salinity variation, and other factors. Some of these diagrams are given in Figs. 19 and 27-30. These zones may be considered in terms of the energy support for the populations. The upper spray zone grows microscopic plants such as blue-green algae and diatoms which are grazed by periwinkles. A few barnacles may set in this zone in exceptional spring tides, but they are so seldom under water that they do not grow appreciably. Next is the zone of regular immersion which supports bright-light-adapted algae, barnacles, oysters, and other organisms capable of existing between periods of immersion and able to filter long enough to grow, but are out of water enough to limit predator consumption. Experiments like that of Crisp (1964; Fig. 31) show the increased growth rates and final weights possible when barnacles are under water for longer periods. In the lower part of the barnacle zone intraspecies competition may be important when predation is restricted. Below this is the zone of brown and red algae, relatively large plants with auxiliary pigments capable of a better growth when suspended in water, but with heavy tissues which are slow to desiccate and which can carry out photosynthesis when exposed. Mussels are associated with this zone, serving as nutrient regenerators.

Seasonal Patterns

The pulse of energy due to light is important to intertidal ecosystems in temperate latitudes, and heating stress in summer restricts inter-tidal development in lower latitudes. The change in sea level with season also controls development of intertidal zones as demonstrated by Stavanger, Norwaz and Breivik (1957) on the coast of Ghana where light and temperature changes are not so important (Fig. 32). Two periods of reproduction and larval releases were found in Miami (Fig. 33) corresponding to spring and fall energy pulses in light energy.

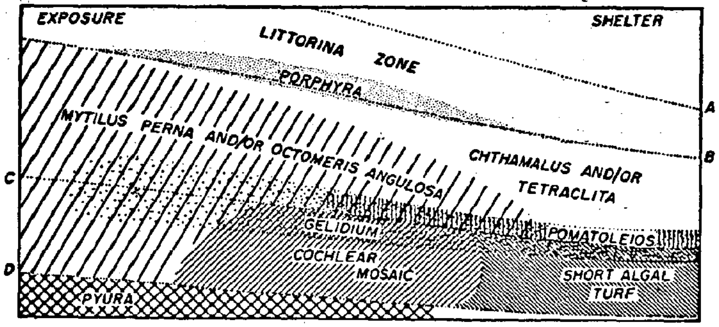
Succession

Lawson (1966) in Figs. 34 and 35 shows algal succession with Enteromorpha first, Ulva next, and other species predominating later. This pattern developed also at Port Aransas, Texas when new jetties of fresh pink granite were added to an existing jetty. In the spring Enteromorpha was first, then massive growths of Ulva, and then brown and red algae characteristic of the old jetty. One factor in the succession was the development of animal populations which grazed the heavy initial growths of greens. For role of grazers controlling the algal composition and of carnivores controlling composition of attached animals, see experimental quadrat studies of Connell (1961) and Castenholz (1967).


Exposure
Shelter
Littoral zone
Maritime zone
Littoral fringe
E.H.W.S.
E.H.W.S
Eulittoral zone
Littoral zone
E.L.W.S.
Sublittoral zone
E.L.W.S.

The proportions and positions of the littoral zones proposed as they may occur around British rocky coasts. Greater variation does exist, however, for on sheltered shores with a large tide range the eulittoral zone may be several times deeper than the littoral fringe, while on exposed shores with a very small tide range or under conditions of greater exposure on mild, northern coasts, the littoral fringe may be several times deeper than the eulittoral zone. Under special, local conditions the upper limit of the sublittoral zone may rise more steeply than that of the eulittoral (after Lewis).

Fig. 24. Change in intertidal zonation bands with exposure to waves (Chapman, 1964)


EXPOSURE
SHELTER
LITTORINA ZONE
PORPHYRA
MYTILUS PERNA AND/OR OCTOMERIS ANGULOSA
CHTHAMALUS AND/OR TETRACLITA
GELIDIUM
POMATOLEIOS
COCHLEAR MOSAIC
SHORT ALGAL TURF
PYURA
A
B
C
D

-Zonation related to exposure in South Africa

Fig. 25 Variation in intertidal zonation bands (Stephenson, 1944).

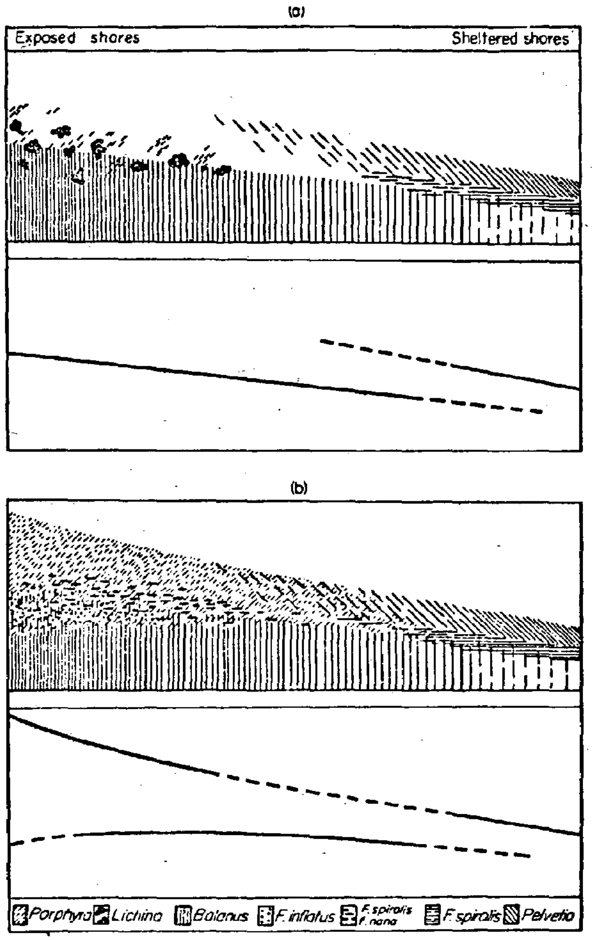

(a)
Exposed shores
Sheltered shores
(b)
Porphyra
Lichina
Balanus
F. inflatus
F. spiralis f. nana
F. spiralis
Pelvetia

Fig. 26. Variation in intertidal zonation bands (Chapman, 1964).

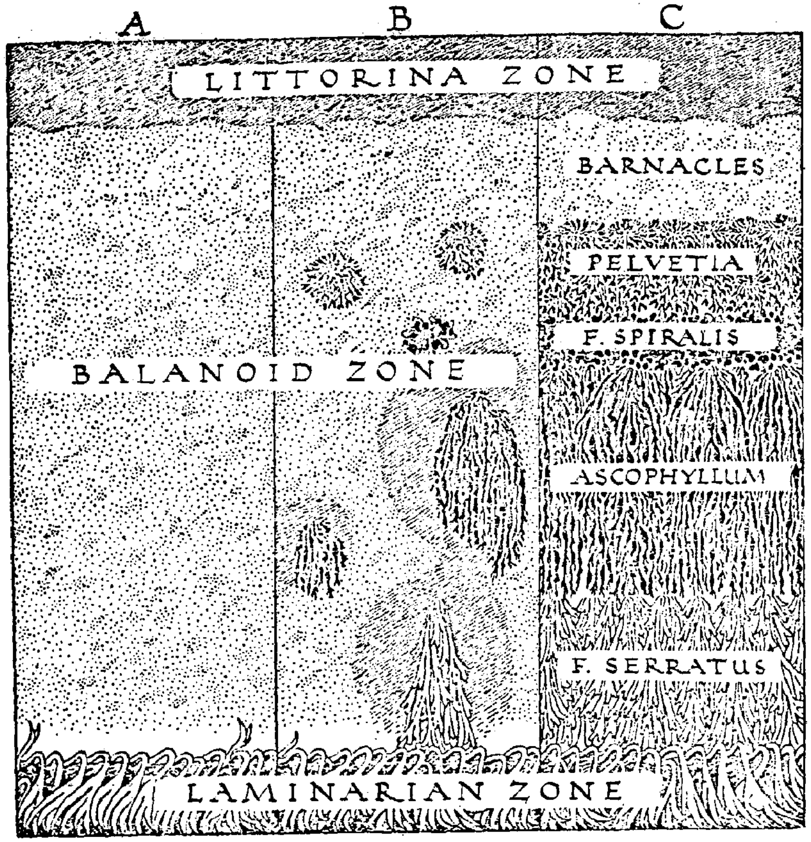

A
B
C
LITTORINA ZONE
BARNACLES
PELVETIA
F. SPIRALIS
BALANOID ZONE
ASCOPHYLLUM
F. SERRATUS
LAMINARIAN ZONE

Diagram illustrating three of the possible types of zonation found on British shores (e.g. on steep rock-faces in Argyllshire). Only part of the width of the *Littorina* and *Laminaria* zones is included. The relative widths of the other zones are accurate for the places chosen. In column B, areas of bare rock (more or less free from barnacles) surround the larger fucoid plants. These areas are due to the movements of the algae when submerged. For column C a locality without *Fucus vesiculosus* or *Porphyra* was chosen. For further explanation see text. (Reproduced from Stephenson, *Journal Linnean Society, Zoology*, Vol. XL, p. 508, by kind permission of the author and of the Linnean Society of London.)

Fig. 27. Atlantic intertidal zonation (From Yonge 1949).

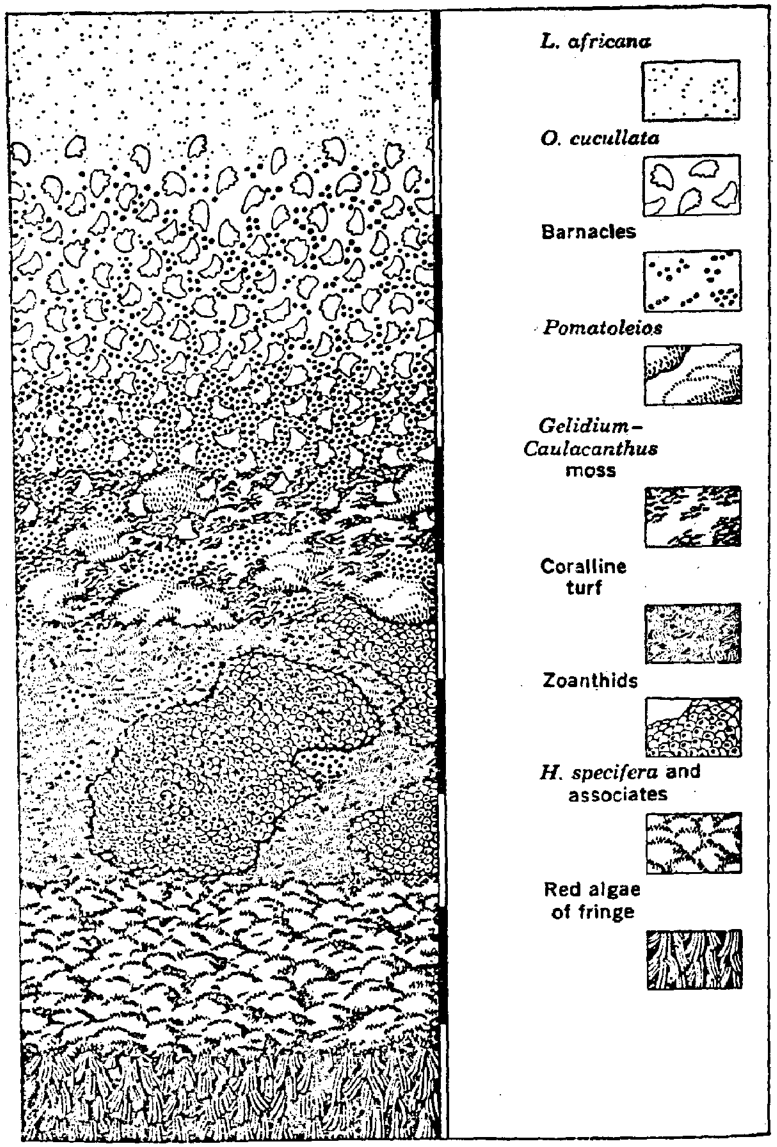

L. africana
O. cucullata
Barnacles
Pomatoleios
Gelidium–Caulacanthus moss
Coralline turf
Zoanthids
H. specifera and associates
Red algae of fringe

Diagram of the zonation on a rocky slope exposed to fairly heavy waves along the subtropical Natal coast. (After Stephenson, 1944.

Fig. 28. Intertidal zonation (From Moore 1958).

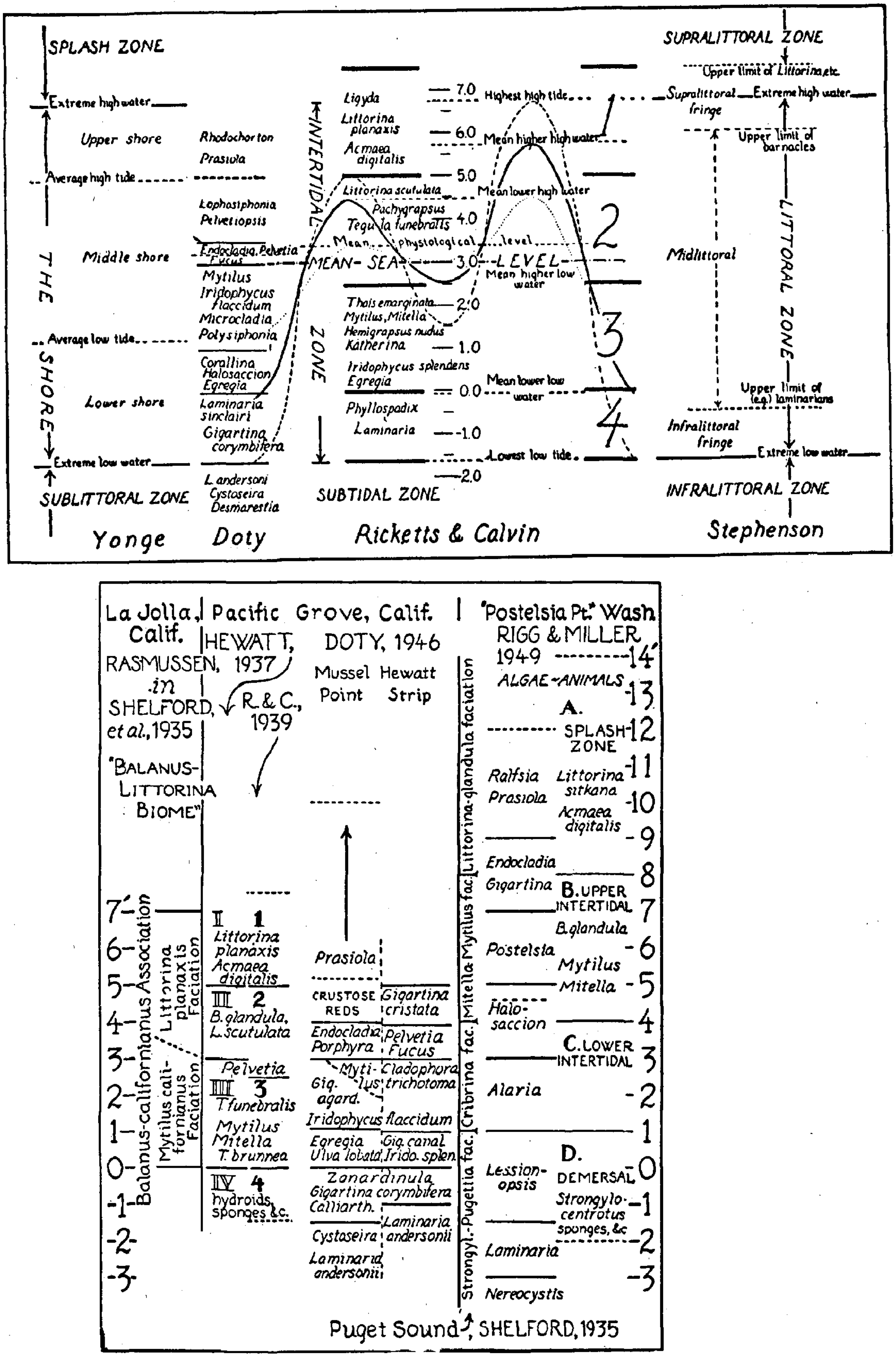
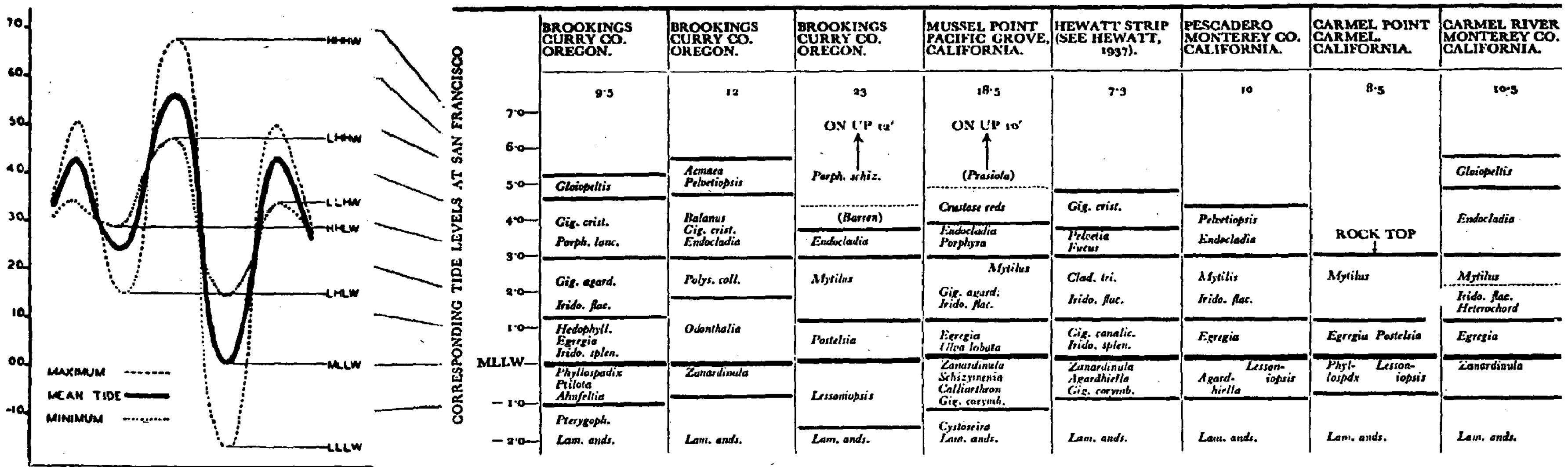

SPLASH ZONE
Extreme high water
Upper shore
Average high tide
THE SHORE
Middle shore
Average low tide
Lower shore
Extreme low water
SUBLITTORAL ZONE
Yonge
Rhodochorton
Prasiola
Lophosiphonia
Pelvetiopsis
Endocladia, Pelvetia
Fucus
Mytilus
Iridophycus flaccidum
Microcladia
Polysiphonia
Corallina
Halosaccion
Egregia
Laminaria sinclairi
Gigartina corymbifera
L. andersoni
Cystoseira
Desmarestia
Doty
INTERTIDAL ZONE
Ligyda
Littorina planaxis
Acmaea digitalis
Littorina scutulata
Pachygrapsus
Tegula funebralis
Mean physiological level
MEAN- SEA- LEVEL
Thais emarginata
Mytilus, Mitella
Hemigrapsus nudus
Katherina
Iridophycus splendens
Egregia
Phyllospadix
Laminaria
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
-1.0
-2.0
Highest high tide
Mean higher high water
Mean lower high water
Mean higher low water
Mean lower low water
Lowest low tide
2
3
4
SUBTIDAL ZONE
Ricketts & Calvin
SUPRALITTORAL ZONE
Upper limit of Littorina, etc.
Supralittoral fringe
Extreme high water
Upper limit of barnacles
Midlittoral
LITTORAL ZONE
Upper limit of (e.g.) laminarians
Infralittoral fringe
Extreme low water
INFRALITTORAL ZONE
Stephenson
La Jolla, Calif.
RASMUSSEN in SHELFORD, et al., 1935
"BALANUS-LITTORINA BIOME"
Pacific Grove, Calif.
HEWATT, 1937
R. & C., 1939
DOTY, 1946
Mussel Point
Hewatt Strip
"Postelsia Pt." Wash.
RIGG & MILLER, 1949
14'
ALGAE - ANIMALS
13
A.
12
SPLASH ZONE
11
10
9
8
7
6
5
4
3
2
1
0
-1
-2
-3
7'
Balanus-californianus Association
Littorina planaxis Faciation
Mytilus californianus Faciation
I 1
Littorina planaxis
Acmaea digitalis
II 2
B. glandula,
L. scutulata
Pelvetia
III 3
T. funebralis
Mytilus
Mitella
T. brunnea
IV 4
hydroids, sponges &c.
Prasiola
CRUSTOSE REDS
Gigartina cristata
Endocladia
Porphyra
Pelvetia
Fucus
Mytilus
Gig. agard.
Cladophora trichotoma
Iridophycus flaccidum
Egregia
Ulva lobata
Gig. canal.
Irido. splen.
Zonardinula
Gigartina corymbifera
Calliarth.
Laminaria andersonii
Cystoseira
Laminaria andersonii
Strongyl.-Pugettia fac.
Cribrina fac.
Mitella-Mytilus fac.
Littorina-glandula faciation
Ralfsia
Prasiola
Littorina sitkana
Acmaea digitalis
Endocladia
Gigartina
B. UPPER INTERTIDAL
B. glandula
Postelsia
Mytilus
Mitella
Halosaccion
C. LOWER INTERTIDAL
Alaria
D. DEMERSAL
Lessoniopsis
Strongylocentrotus
sponges, &c
Laminaria
Nereocystis
Puget Sound, SHELFORD, 1935

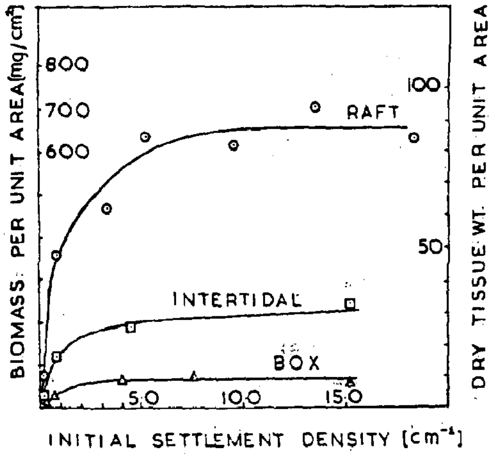
Fig. 29. Comparison of intertidal zonation of different authors



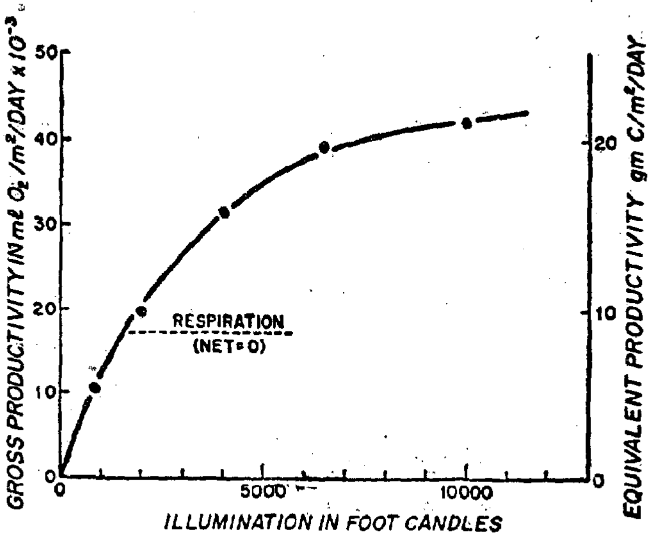
Clad. tri. = *Cladophora trichotoma*, *Gig. agard.* = *Gigartina agardhii*, *Gig. canalic.* = *Gigartina canaliculata*, *Gig. corymb.* = *Gigartina corymbifera*, *Gig. crist.* = *Gigartina cristata*, *Hedophyll.* = *Hedophyllum sessile*, *Irido. flac.* = *Iridiophycus flaccidum*, *Irido. splen.* = *Iridophycus splendens*, *Lam. andrs.* = *Laminaria andersonii*, *Polys. coll.* = *Polysiphonia collinsii*, *Porph. lanc.* = *Porphyra lanceolata*, *Porph. schiz.* = *Porphyra schizophylla*, *Pterygoph.* = *Pterygophora californica*.

The algal zonation on some Pacific coast shores in relation to tide levels at San Francisco.
(From Doty, 1946.)

Fig. 30. Comparison of intertidal zonation (From Doty, 1946).

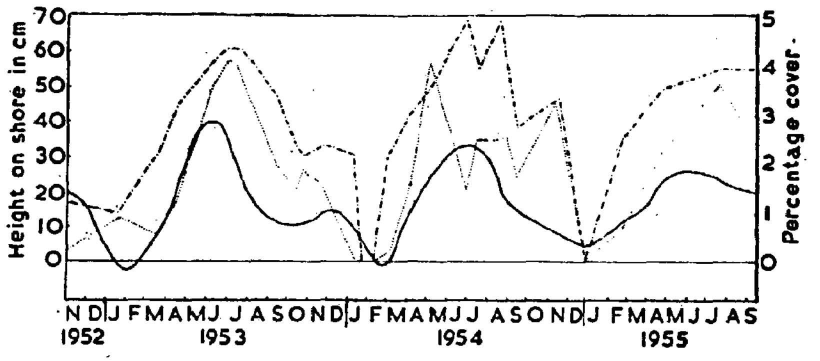


The relationship between total barnacle biomass (dry weight) per unit area at the end of the first growing season and the initial settlement density of cyprids in each of the three environments.



—Gross productivity and light intensity for *Fucus vesiculosus*; measurements made under a bell jar on a natural shore population.

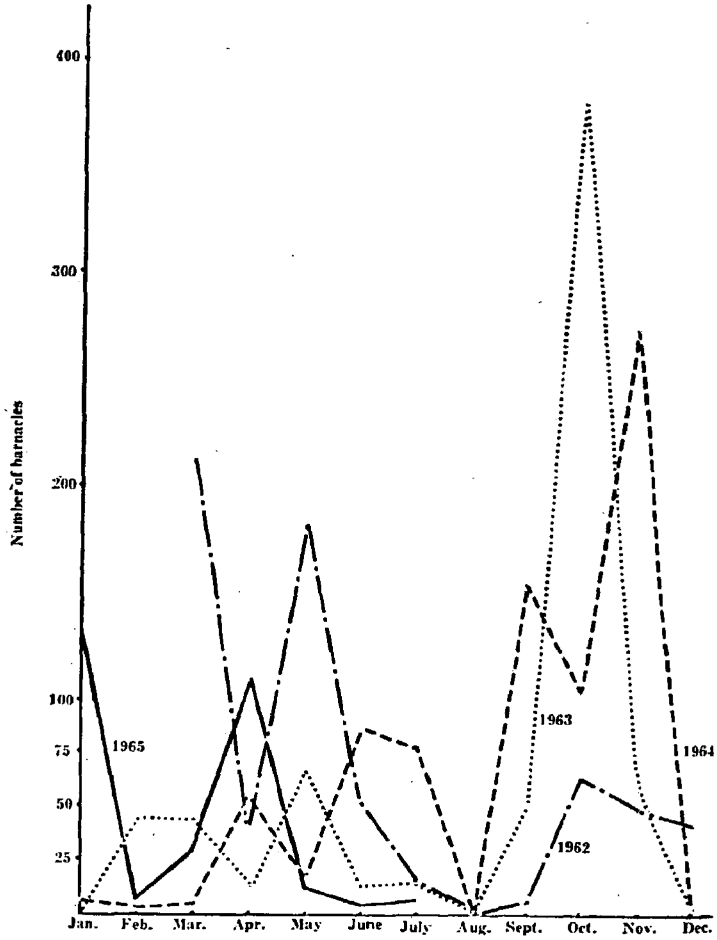
Fig. 31. Barnacle accumulation for surfaces exposed to different volumes of water (From Crisp 1964).



Relationship between seasonal tidal changes and the zonation and quantity of *Hypnea musciformis* at a station on the coast of Ghana. Continuous line is the tidal curve of the heights of the lowest of the low waters in each month. The broken line represents the seasonally fluctuating upper limit of *Hypnea* and the dotted line the percentage cover of *Hypnea*.

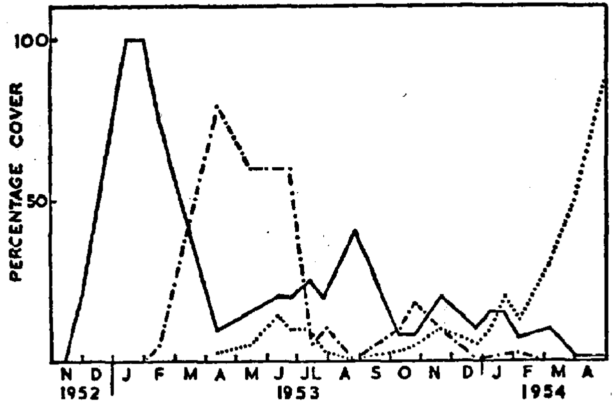
(After Lawson, 1957.)

Fig. 32. Seasonal patterns in Africa (Lawson, 1957).

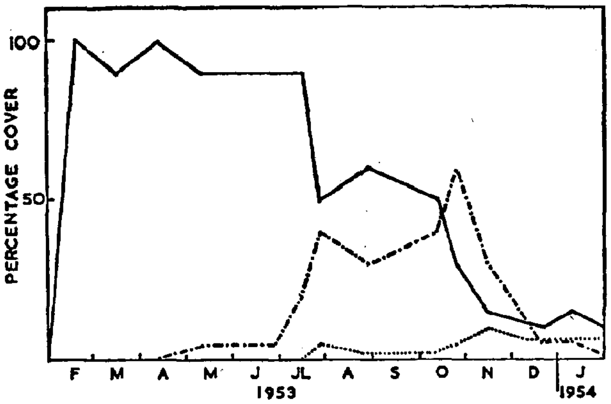


Settlement of *Balanus trigonus* on glass panels at the Miami Marin Research and Test Station, Miami Beach, March 1962 to July 1965.

Fig. 33. Seasonal patterns in barnacle reproduction in Miami (Werner, 1967).



–Diagram to show the behaviour of some of the algae recolonizing the upper of four denuded quadrats at Christiansborg, Ghana. The continuous line represents *Enteromorpha* and *Ulva fasciata*. In the first few weeks *Enteromorpha* dominated the cleared area but soon it was mixed with and replaced by *Ulva*. The broken line represents lithothamnia, and the dotted line *Chaetomorpha antennina* (after Lawson, 1954c).



—Diagram to show recolonization at Christiansborg, Ghana, on a quadrat denuded nearly three months later than that given in Fig. 3, but on the same level on the shore. Key as for Fig. 3.

Fig. 34-35. Recolonization sequences (Lawson, 1966).

Chapter A-2

HIGH ENERGY BEACHES

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INTRODUCTION

High energy beaches are sandy shores which receive strong wave action. Wind-driven waves and currents pound the coast, and the hydrodynamics of these waves, plus the daily ebb and flow of tides, sort the sand into zones of coarser and finer particles. Fig. 1 shows the major zones in a beach environment.

This special ecosystem, with its shifting sands and pounding waves, includes a very specialized biota, the sand dwellers or psammon. Some of the sand fauna are found entirely below the water line, some high on the beach, and some at the drift line where organic rubbish accumulates. The epipsammon (shorebirds, fishes, certain beetles, etc.) live on the sand surface; the endopsammon (snails, bivalves, crustacea, etc.) burrow beneath the surface; and the mesopsammon (diatoms, ciliates, tardigrades, turbellarians, gastrotrichs, gnathostomulids, copepods, etc.) live between the sand grains. The beach with its sand fauna forms an extensive food filtering system, taking from the inrushing water nutrients in the form of detritus, possibly dissolved materials, and planktonic or larger organisms.

Some of the macrofauna of sand beaches are shown in Fig. 2 taken from Pearse, Humm, and Wharton's (1942) paper on the ecology of sand beaches at Beaufort, North Carolina. Interstitial fauna are shown in Figs. 3 and 4 from the papers of Delamare (1960) and Ax (1966). Special locomotory, respiratory, and morphological adaptations permit the psammon to inhabit a shifting environment that may be alternately flooded and exposed to desiccation, where oxygen tension may be low, and where waves beat ceaselessly.

EXAMPLES OF HIGH ENERGY BEACH SYSTEMS

Some examples of much-studied beach systems are the following.

Gulf Coast: Port Aransas, Texas

A map of the Port Aransas beach area and a typical beach profile are given in Figs. 5 and 6. In summer, especially, there are steady southeast winds creating a stable beach structure and a long shore current running northward. Figs. 7 - 9 and Tables 1 - 4 show seasonal variations for a number of parameters in the surf zone at Port Aransas: temperature and salinity, fish populations,

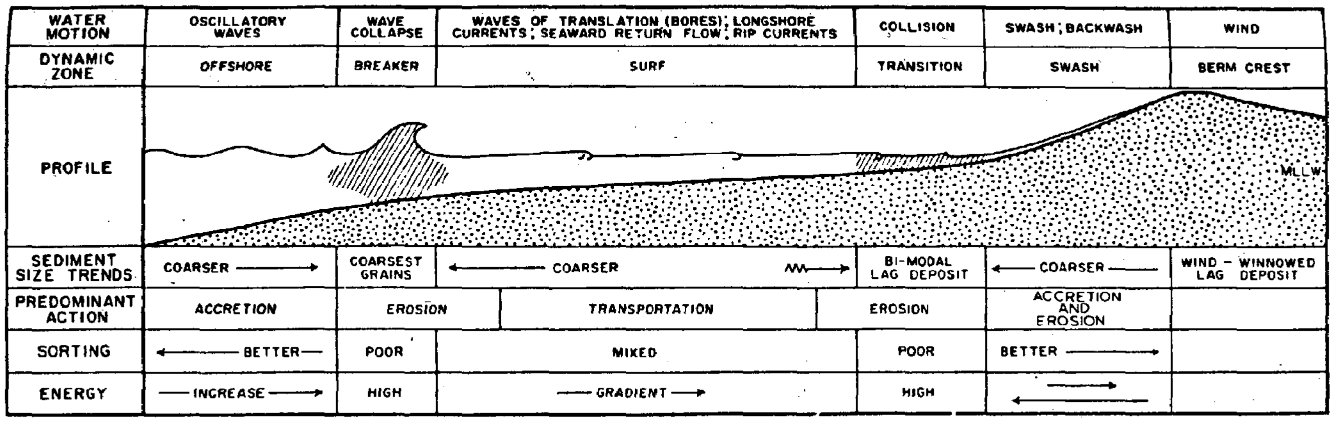

WATER MOTION
OSCILLATORY WAVES
WAVE COLLAPSE
WAVES OF TRANSLATION (BORES); LONGSHORE CURRENTS; SEAWARD RETURN FLOW; RIP CURRENTS
COLLISION
SWASH; BACKWASH
WIND
DYNAMIC ZONE
OFFSHORE
BREAKER
SURF
TRANSITION
SWASH
BERM CREST
PROFILE
MLLW
SEDIMENT SIZE TRENDS
COARSER
COARSEST GRAINS
COARSER
BI-MODAL LAG DEPOSIT
COARSER
WIND - WINNOWED LAG DEPOSIT
PREDOMINANT ACTION
ACCRETION
EROSION
TRANSPORTATION
EROSION
ACCRETION AND EROSION
SORTING
BETTER
POOR
MIXED
POOR
BETTER
ENERGY
INCREASE
HIGH
GRADIENT
HIGH

Fig. 1: Schematic diagram of a high energy beach environment showing major zones relating to sand motion. Cross hatching indicates zones of high concentrations of suspended sand grains (From Ingle 1966; Fig. 116).

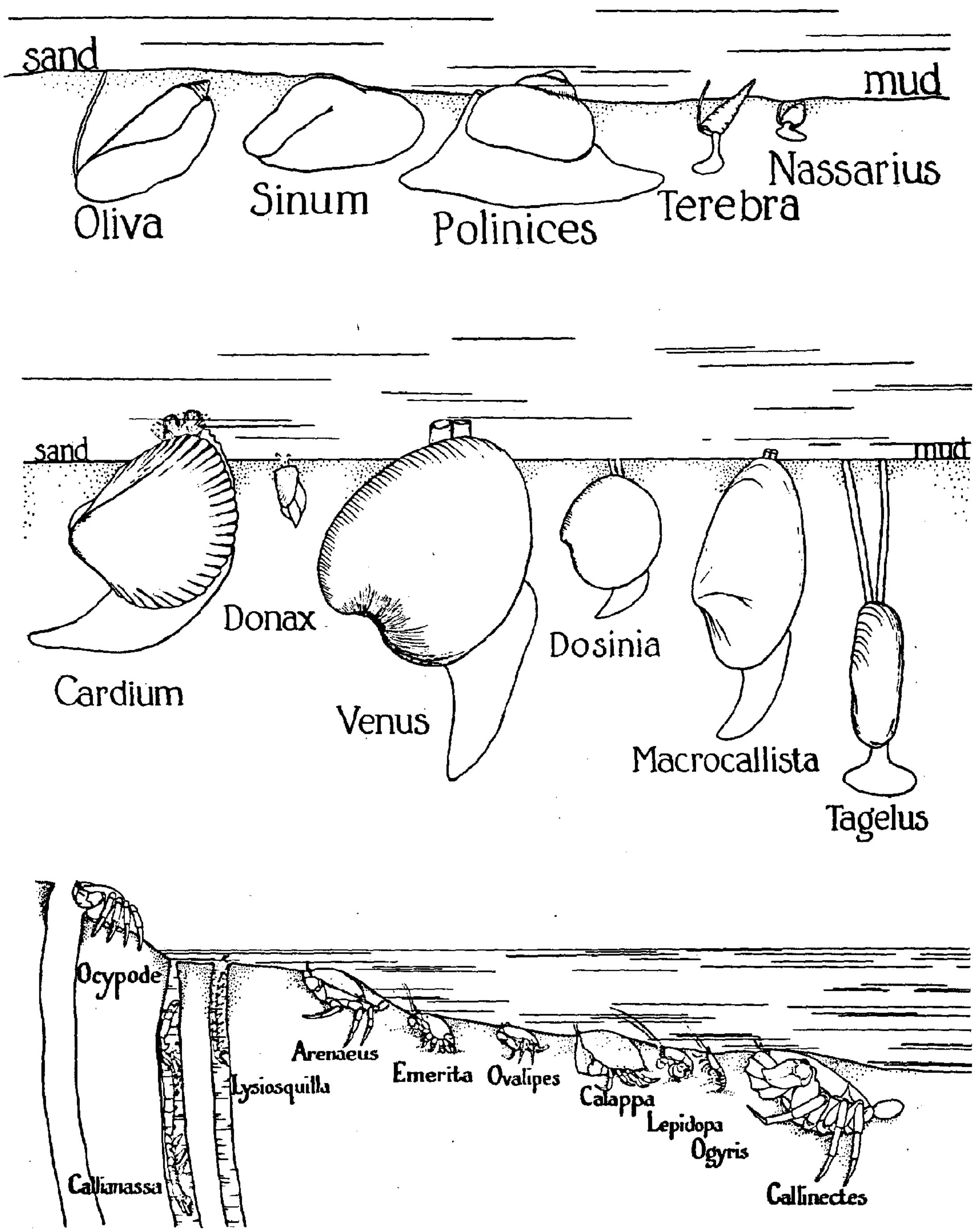
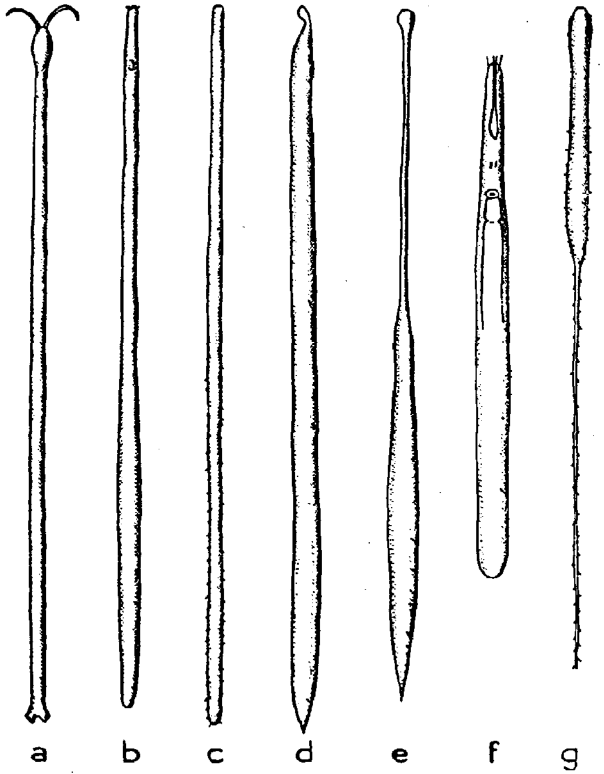
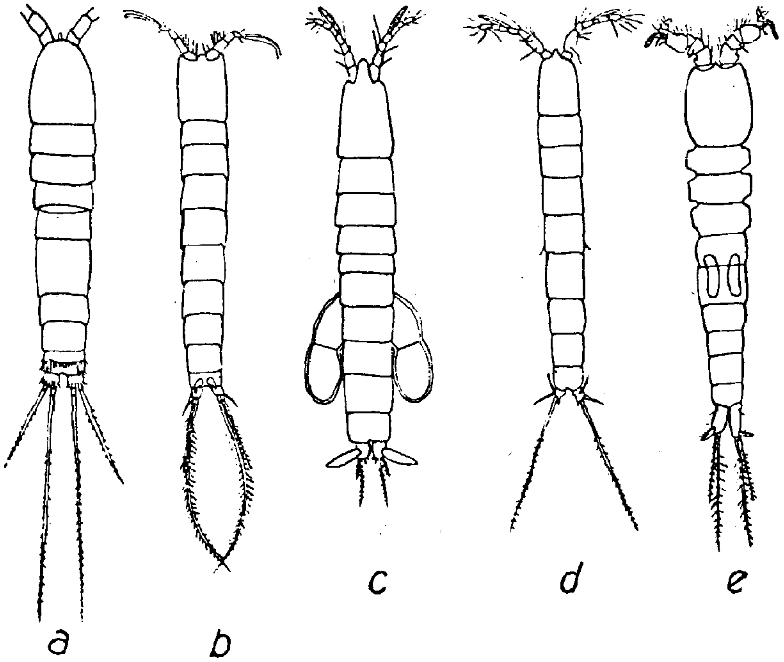

sand
mud
Oliva
Sinum
Polinices
Terebra
Nassarius
sand
mud
Cardium
Donax
Venus
Dosinia
Macrocallista
Tagelus
Ocypode
Callianassa
Lysiosquilla
Arenaeus
Emerita
Ovalipes
Calappa
Lepidopa
Ogyris
Callinectes

Fig. 2: Macrofauna (endopsammon) of sand beaches at Beaufort, N.C. Burrowing snails, bivalves, and crustacea. (From Pearse, Humm, and Wharton, 1942; Figs. 4, 8, and 10.)

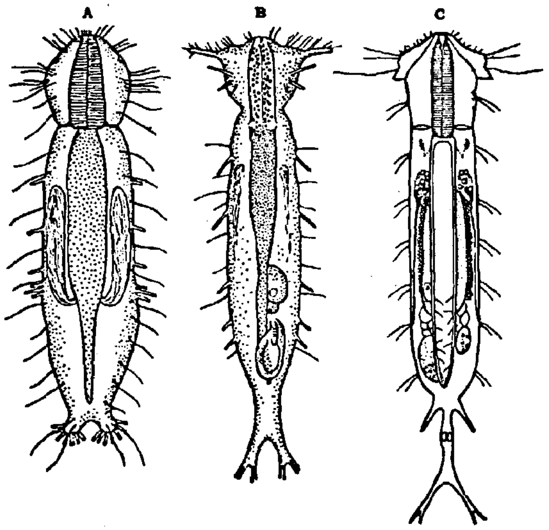


- Convergence chez divers groupes interstitiels. — *a*, *Protodrilus chaetifer* (Archiannélide). — *b*, *Coelogynopora* sp. (Turbellarié). — *c*, *Michaelsena* (Oligochète). — *d*, Cilié. — *e*, *Trachelocerca* (Cilié). — *f*, *Proschizorhynchus oculatus* (Turbellarié Rhabdocoele). — *g*, *Urodasys mirabilis* (Gastrotriche) (d'après Remane, 1953).

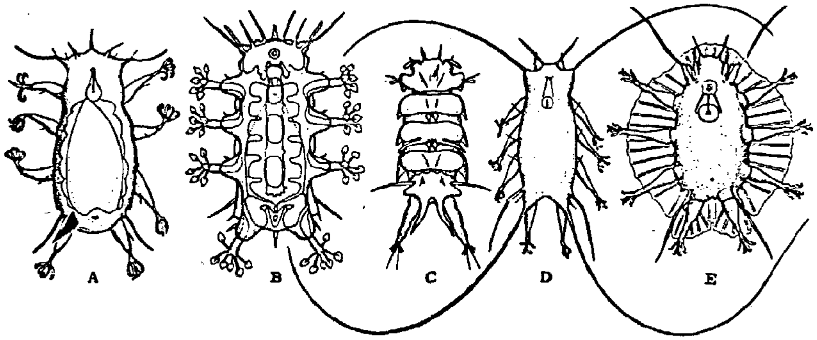


- *Copépodes psammiques marins* (d'après Wilson). — *a*, *Nitocra chelifer*, femelle, vue dorsale. — b, *Arenosetella spinicauda*, mâle. — c, *Goffinella stylifer*, montrant les ovicacs appliqués et les œufs de grande taille. — d, *Paraleptastacus brevicaudatus*, femelle. — e, *Emertonia gracilis*, mâle.

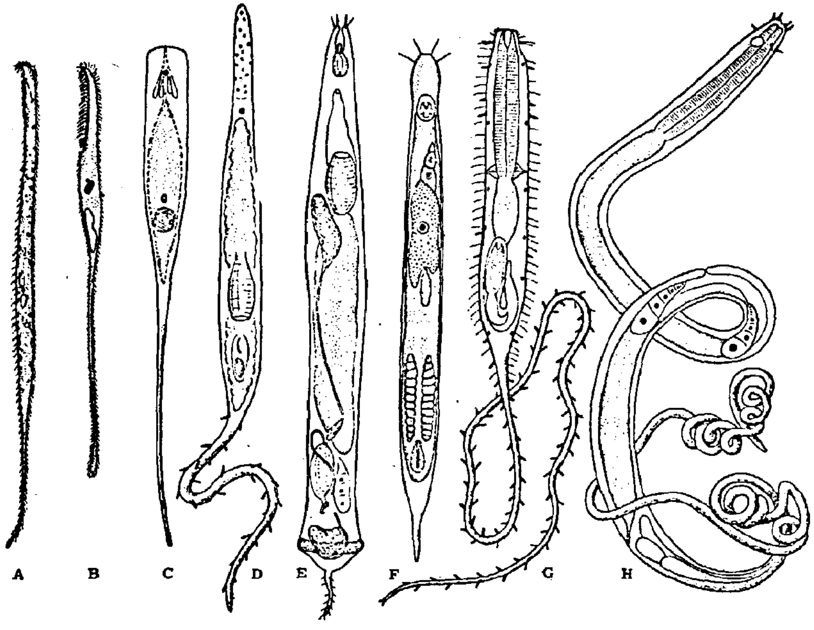
Fig. 3: Mesopsammon (archiannelids, turbellarians, oligochaetes, gastrotrichs, and copepods), minute organisms which live between the sand grains on beaches (From Delamare 1960; Figs 44 and 85).



Gastrotrichen der Ordnung Macrodasyoidea. Differenzierung eines Gabelschwanzes in der Familie Dactylopodaliidae. A) *Dactylopodalia baltica* Remane, B) *Dactylopodalia cornuta* Swedmark, C) *Dendrodasys gracilis* Wilke (aus Ax 1963).



Mesopsammale Tardigraden der Ordnung Arthrotardigrada. A) *Halechiniscus subterraneus* Renaud-Debyser, B) *Batillipes mirus* Richters, C) *Stygarctus bradypus* Schulz, D) *Tanarctus tauricus* Renaud-Debyser, E) *Actinarctus doryphorus* Schulz (nach Renaud-Debyser, 1949b, Marcus 1936, Schulz 1951, Grell 1937).



Differenzierung eines Schwanzfadens in der interstitiellen Sandfauna. A) *Remanella caudata* Dragesco (Ciliata), B) *Spirostomum filum* (Ehrbg.) Pénard (Ciliata), C) *Mecynostomum filiferum* Ax (Turbellaria Acoela), D) *Boreocelis urodasyoides* Ax (Turbellaria Proseriata), E) *Cheliplanilla caudata* Meixner (Turbellaria Kalyptorhynchia), F) *Gnathostomula paradoxa* Ax (Gnathostomulida), G) *Urodasys viviparus* Wilke (Gastrotricha Macrodasyoidea), H) *Trefusia longicauda* (de Man) (Nematodes). — (nach verschiedenen Autoren aus Ax 1963).

Fig. 4: Mesopsammon or interstitial sand fauna (Gastrotrichs, tardigrades, ciliates, turbellarians, gnathostomulids, nematodes) (From Ax 1966; Figs. 3, 4, and 14).

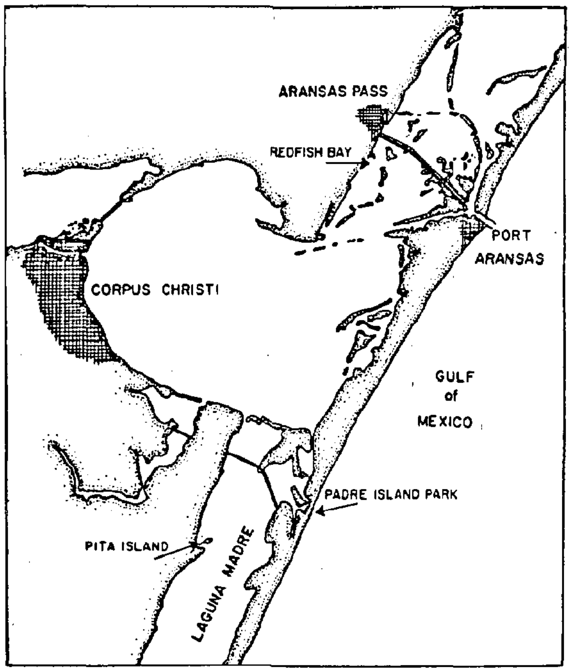

ARANSAS PASS
REDFISH BAY
PORT ARANSAS
CORPUS CHRISTI
GULF of MEXICO
PADRE ISLAND PARK
PITA ISLAND
LAGUNA MADRE

Fig. 5: Map of Port Aransas, Texas beach area representing a high energy beach system (From Oppenheimer and Jannasch 1962; Fig. 1).

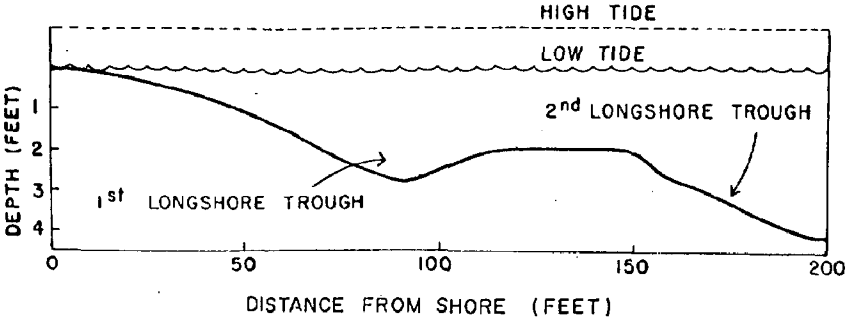


Fig. 6: Typical beach profile south of Port Aransas on Mustang Island, Texas (From McFarland 1963a; Fig. 1).

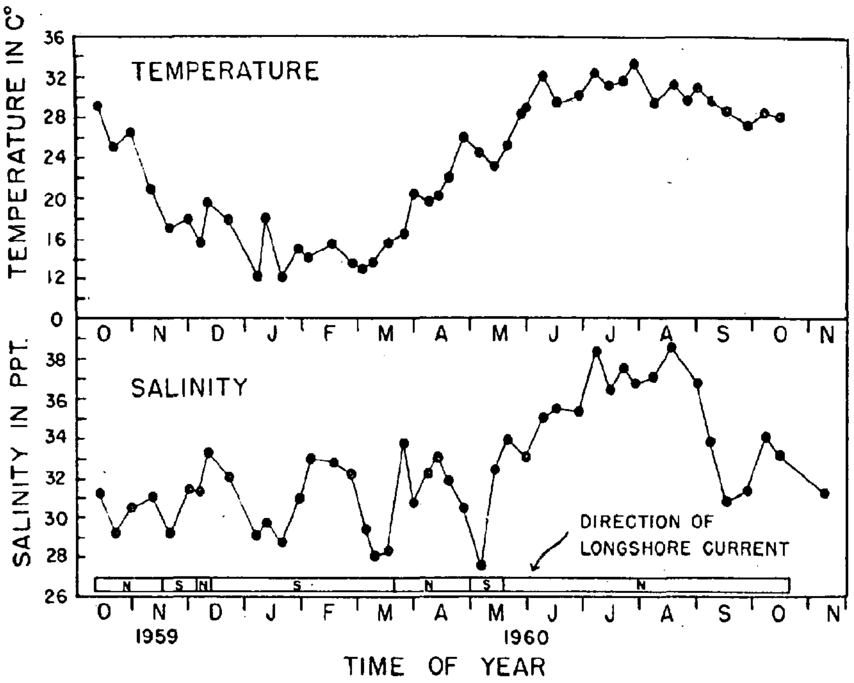


Fig. 7: Seasonal changes in temperature and salinity of the surf zone of Mustang Island, Texas (south of Port Aransas). (From McFarland 1963a; Fig. 2.)

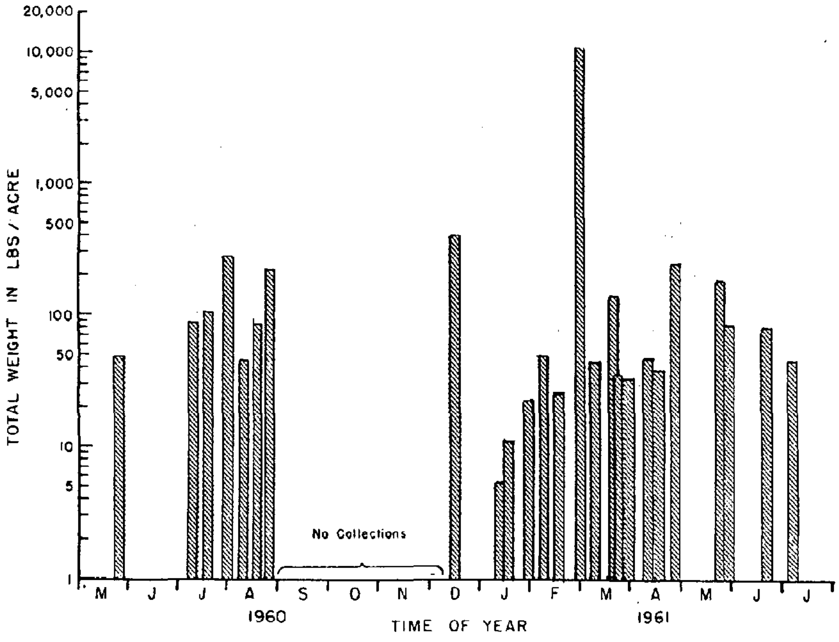


Fig. 8: Seasonal changes in fish biomass (pounds per acre) in the surf fringe at Mustang Island, Texas. High values for December 15, 1960 and March 1, 1961 represent mostly specimens of Mugil cephalus and Galeichthys respectively (From McFarland 1963b; Fig. 1).

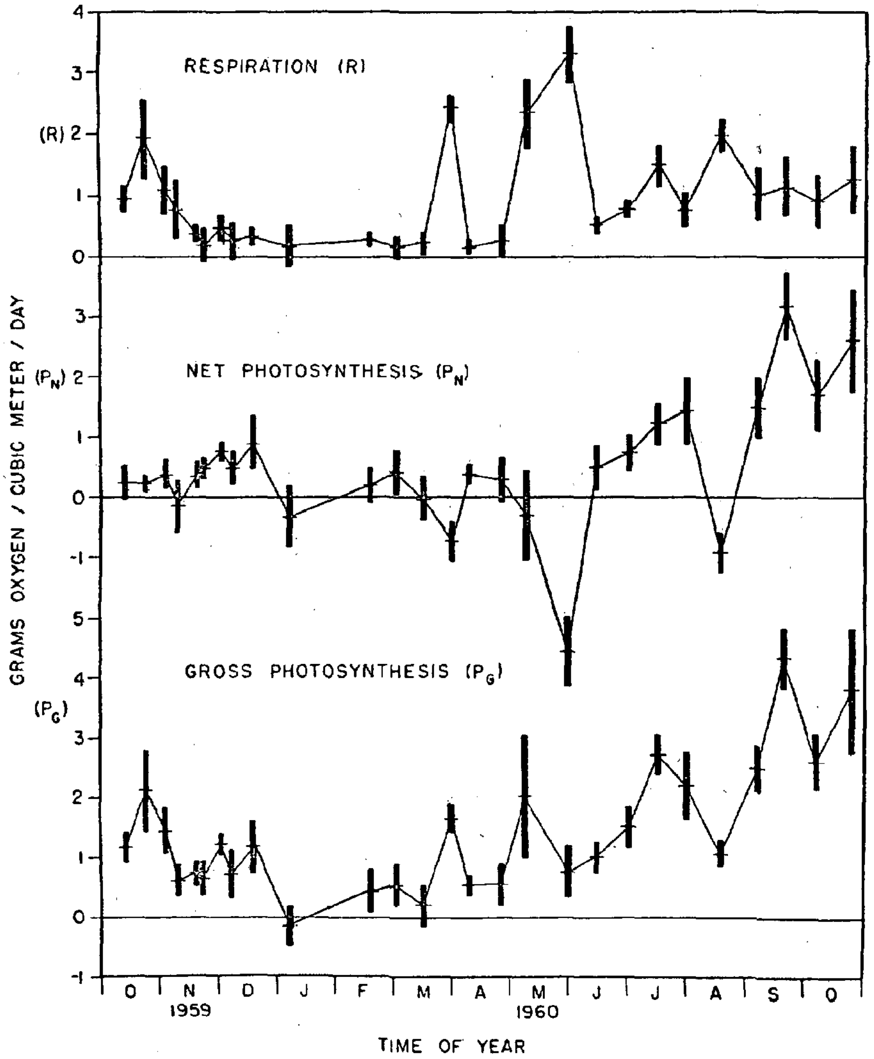


Fig. 9: Seasonal changes in plankton production in the surf of Mustang Island (Port Aransas), Texas, as obtained by the light-dark bottle method. Means and 95% confidence intervals are shown (From McFarland 1963a; Fig. 4).

Table 1: Total numbers per acre of each species of fish (and all species) caught in the surf fringe of Mustang Island (Port Aransas, Texas) on various dates through the years 1960 and 1961 (From McFarland 1963b; Table 1).

Species	Date of Collection																								
	May 25	July 12	July 19	July 29	Aug. 10	Aug. 18	Aug. 26	Dec. 15	Jan. 13	Jan. 18	Jan. 31	Feb. 9	Feb. 17	Mar. 1	Mar. 10	Mar. 20	Mar. 24	Mar. 29	Apr. 11	Apr. 18	Apr. 28	May 26	May 31	June 22	July 7
Scoliodon terranovae	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	....	8	....
Sphyrna tiburo	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	4	....
Narcine braziliensis	1	1	....	1	....	2	1	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Dasyatis americana	....	....	....	....	....	....	9	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Dasyatis sabina	1	1	3	....	15	39	90	....	....	....	....	....	....	....	....	....	....	1	....	14	18	13	....	41	20
Rhinoptera bonasus	....	....	....	....	....	8	8	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Elops saurus	4	....	4	8	1	5	3	....	....	....	....	6	....	....	....	....	....	....	....	....	....	7	....	1	....
Harengula pensacolae	....	....	1	....	....	....	....	....	....	....	....	....	....	....	....	7	284	133	1	4	....	3	11	6	74
Brevoortia patronus	2	19	1	....	....	2	9	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Anchoa sp.	....	....	....	....	....	....	....	....	....	....	....	3	....	....	8	9	148	32	167	9	....	....	....	16	....
Galeichthys felis	7	19	....	....	19	24	60	38	1	10	....	9	104	a*	27	2	2	2	....	1	....	15	5	....	23
Strongylura marina	....	1	1	....	....	1	1	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Syngnathus sp.	....	....	....	....	....	....	....	....	....	....	....	....	6	....	....	....	1	....	1	1	2	....	....	....	....
Mugil cephalus	20	93	13	75	17	4	345	480	7	15	45	72	4	8	9	3	32	60	99	7	605	25	16	10	19
Menidia beryllina	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1919	....	....	132	99	205	....	....	5	....
Polydactylus octonemus	277	1061	2503	2197	47	83	55	....	....	....	....	....	....	....	....	....	85	330	1118	275	....	143	1923	....	38
Centropomus undecimalis	1	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....
Pomatomus saltatrix	4	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	11	6	9	6	2	....
Elagatis bipinnulatus	....	....	....	....	....	3	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Trachinotus carolinus	124	55	40	....	34	23	62	....	....	....	....	....	....	4	14	68	2	....	....	1	13	....	5	57	42
Caranx bartholomaei	....	1	....	49	....	....	....	....	....	5	....	....	....	....	1	....	....	....	....	....	....	....	....	....	....
Caranx hippos	....	....	38	47	3	2	12	....	....	....	....	....	....	....	....	....	....	....	....	....	1	1	20	8	47
Chloroscombrus chrysurus	8	....	....	....	3	....	....	....	....	....	....	....	....	....			1	....	....	....	31	220	780	20	5
Selene vomer	2	....	....	....	2	....	1	....	....	....	....	....	....	....	....	....	....	....	....	....	1	2			

a* 35,881 catfish.

Table 1: Continued

Species	Date of Collection																								
	May 25	July 12	July 19	July 29	Aug. 10	Aug. 18	Aug. 26	Dec. 15	Jan. 13	Jan. 18	Jan. 31	Feb. 9	Feb. 17	Mar. 1	Mar. 10	Mar. 20	Mar. 24	Mar. 29	Apr. 11	Apr. 18	Apr. 28	May 26	May 31	June 22	July 7
Eucinostomus argenteus	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1
Conodon nobilis	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	429	....	....	15
Bairdiella chrysura	....	....	....	....	....	....	....	....	8	8	....	42	....	....	16	13	1	12	1	22	2	....	....	....	....
Sciaenops ocellata	....	1	....	....	1	....	1	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Leiostomus xanthurus	75	....	10	26	42	27	57	....	....	....	....	....	....	....	....	26	....	....	....	....	....	10	....	....	....
Micropogon undulatus	2	7	....	....	....	....	....	....	....	....	....	....	....	....	3	....	....	....	....	....	....	....	....	....	....
Menticirrhus americanus	23	....	....	....	....	....	....	....	....	....	....	....	....	....	5	....	....	....	....	....	....	....	....	....	....
Menticirrhus atlanticus	....	....	....	....	....	....	....	....	....	....	....	....	....	3	....	....	....	....	....	....	....	1	....	200	....
Menticirrhus littoralis	....	36	136	154	247	54	401	....	....	....	....	....	8	....	....	11	16	31	10	25	77	40	25	111	77
Pogonias cromis	....	....	....	....	....	....	4	....	....	....	....	....	....	....	....	53	4	4	....	1	1	2	3	3	4
Cynoscion nebulosus	2	1	....	2	2	3	2	....	....	....	....	....	....	17	....	....	....	....	....	....	....	1	....	1	1
Lagodon rhomboides	3	39	....	5	5	....	2	2	....	....	26	10	....	....	1	59	1	4	9	7	13	91	25	2	28
Archosargus probatocephalus	....	....	3	2	3	6	2	....	....	3	....	....	....	....	1	1	1	1	....	2	7	....	....	6	3
Chaetodipterus faber	1	1	....	....	1	2	1	....	....	....	....	....	....	....	....	....	....	5	1	11	13	4	....	....	19
Trichiurus lepturus	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	2	....	....	....	....	....
Scomberomerus maculatus	....	1	....	....	1	2	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....	1	....	10	....
Peprilus paru	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	168	....	....	....	....	....
Paralichthys lethostigma	11	....	....	....	1	1	....	....	....	....	....	....	....	....	....	1	....	....	6	2	5	2	....	....	....
Filefish	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	3
Lactophrys tricornis	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	....
Sphaeroides nephelus	....	....	....	....	....	....	....	25	....	3	....	....	....	....	2	....	....	2	....	....	....	....	....	....	....
Opsanus beta	....	....	....	....	....	....	....	....	....	....	....	8	....	....	....	....	....	....	....	....	....	....	....	....	....
Histrio histrio	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	11	....	....
Totals	568	1335	2754	2564	444	290	1126	547	16	44	71	151	122	35913	87	2172	579	617	538	662	1001	1020	2830	508	419

Table 2: Seasonal changes in net plankton at Mustang Island (Port Aransas, Texas) during spring, summer and fall of 1960. Nonbracketed values are the average numbers of individuals per cubic meter of water. Bracketed values are the ranges for replicate samples. Each mean represents 4 samples. The sample for August 17, 1960 represents only 2 samples. (From McFarland 1963 a; Table 3.)

General type of animal	Date, 1960													
	Mar. 9	Mar. 16	Mar. 23	Apr. 13	May 13	May 31	June 17	July 16	July 29	Aug. 17	Sept. 6	Sept. 20	Oct. 6	Oct. 19
Comb jellies	0.3 (0–1.0)	0.2 (0–0.6)	....	....	....	....	....	....	1.9 (0–3.9)	....	....	....	....	....
Veliger larvae	....	....	....	....	1.0 (0–2.1)	....	....	....	....	....	....	....	....	0.3 (0–0.9)
Bryozoa	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Chaetognatha	....	....	....	....	....	....	....	....	....	....	....	....	3.6 (2.8–4.1)	16.3 (9.4–27.3)
Mysids	....	....	....	0.2 (0–0.8)	0.8 (0–2.1)	....	....	....	....	....	1.3 (1.0–1.5)	5.0 (3.1–6.4)	....	....
Isopods	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Amphipods	....	....	....	....	0.7 (0–2.8)	9.8 (9.5–16.6)	....	....	....	....	....	....	....	....
Copepods	1.2 (0–4.0)	....	....	19.7 (1.3–42.1)	15.7 (8.6–26.9)	3.9 (2.3–6.6)	7.8 (0.5–8.0)	....	....	0.7 (0.5–0.8)	0.3 (0–1.0)	41.3 (27.0–67.0)	5.5 (2.8–7.6)	34.0 (25.5–38.7)
Shrimp larvae	4.2 (2.2–7.7)	5.9 (0–13.0)	....	....	....	....	2.1 (0.8–3.6)	....	0.2 (0–0.5)	....	1.3 (0–4.0)	....	....	....
Crab larvae	79.1 (34.0–129.4)	146.5 (19–326.0)	5.9 (1.4–12.5)	0.4 (0–0.7)	0.9 (0–2.3)	....	0.1 (0–0.4)	....	....	....	0.9 (0–2.0)	....	....	....
Fish larvae	33.2 (7.4–97.0)	4.5 (0.4–9.8)	....	2.6 (0–3.9)	....	....	....	....	....	....	....	....	....	0.3 (0–1.0)
Totals	118.0	157.1	5.9	22.9	19.1	13.7	10.0	0.0	2.1	0.7	3.8	46.3	9.1	60.6

Table 3: Estimated dry weight of Donax meat and shell in grams per linear mile of beach at Mustang Island (Port Aransas, Texas) (From Loesch 1957; Table 7).

Date	Stations					
	1	2	3	4	5	Average
Meat:						
June 27, 1951	422	440	246	246	282	327
August 3, 1951	299	317	88	246	229	236
September 3, 1951	.....	......	176	88	35	100
September 29, 1951	5.3	1.8	1.8	1.8	7.0	3.5
November 17, 1951	Concentrations could not be determined.					
December 16, 1951	Concentrations could not be determined.					
June 2, 1952	352	229	229	950	154	405
June 27, 1952	18	53	123	158	194	109
Shell:						
June 27, 1951	8,018	8,360	4,654	4,654	5,358	6,346
August 3, 1951	5,591	6,023	1,672	4,654	4,351	4,351
September 3, 1951	..	..	3,334	1,672	665	2,014
September 29, 1951	103	34	34	34	133	66
November 17, 1951	Concentrations could not be determined.					
December 16, 1951	Concentrations could not be determined.					
June 2, 1952	6,688	5,681	4,351	18,050	3,686	7,695
June 27, 1952	334	1,007	2,337	3,002	3,686	2,014

Table 4: Observed predators of Donax at Mustang Island (Port Aransas, Texas) (From Loesch 1957; Table 8).

Predator	*Comments*
Birds	
Catoptrophorus semipalmatus (Eastern willet)	Stomach analysis, 4 of 6 contained *Donax*
Crocethia alba (Sanderling)	Observed eating *Donax* on beach
Squatarola squatarola (Black bellied plover)	Stomach analysis, 1 of 1 contained *Donax*
Fish	
Menticirrhus spp. (Whiting)	Stomach analysis, 1 of 5 contained *Donax*
Leiostomus xanthurus (Spot)	Stomach analysis, 2 of 6 contained *Donax*
Pogonias cromis (Drum)	Stomach analysis, 2 of 9 contained *Donax*
Crabs	
Callinectes sapidus (Blue)	Frequently observed eating *Donax*
Arenaeus cribrarius (Spotted)	Observed eating *Donax*
Ocypode albicans (Ghost)	Observed handling *Donax* at night
Boring Snails	
Thais floridana (Conch)	Observed holding *Donax;* although drilling was not observed, many drilled shells were found.
Oliva spp.	
Natica duplicata (Moonshell)	

phytoplankton productivity, and clam (Donax) populations. Table 4 lists observed Donax predators.

East Coast: Beaufort, N. C.

Some of the sandy beaches in the Beaufort area are shown in Fig. 10. The outer banks (Bogue, Shackleford) are examples of high energy beaches, while Bird Shoal, Shark Shoal, Pivers Island (location of the Duke Marine Station), etc. are more sheltered. Diurnal variations in temperature, vapor pressure, and evaporation rate for a Pivers Island beach were measured by Barnes and Barnes during their study of driftline spiders (Fig. 11). Fig. 12 is a comparison of night and day activity of spiders beneath and outside the drift at Pivers Island. Fig. 13 gives carapace length frequency of the little mole crab, Emerita talpoida, collected on three occasions in the summer of 1940. Table 5 lists the organisms caught in seine hauls and rake nets on sand beaches of the Beaufort area in 1939 and 1941 in the study by Pearse, Humm and Wharton (1942). Table 6 gives seasonal data for shell length for Donax and Olivella. Table 7 shows the condition of female Emeritas (with eggs and/or male) at different time periods.

PHYSICAL ASPECTS OF HIGH ENERGY BEACHES

Occurrence

Sandy beaches are found on all continents and on most islands. Their occurrence is related to coastal age, to local hydrodynamics, and to sedimentary processes.

Coastal age depends on the movement of sea level relative to land (Fig. 14). This results in large part from isostatic changes — an effect of storing and releasing great ice masses at both poles. Beach formation and physical structure are based on wave energies and highly selected sediments which form the inorganic subsystem. These, in turn, are derived from the conversion of solar energy into the dynamics of atmospheric pressure patterns, part of whose energy is transferred to waves. In open ocean, with a fetch or runway of over a thousand miles, waves grow to maximal dimensions. From stormy areas they travel as swells with increasing speed, crashing finally against coastlines where they release their energy in erosion or particle sorting effects. Of all sediments known, sand (particularly that of medium size) is most easily eroded. Silt and clay, as well as gravel and cobble, resist erosion, but sand is transported. Since sand has nearly similar erosion and sedimentation speeds, sandy coasts are by far the most common systems in coastal morphology.

Young coasts (Fig. 14) are those that are recently sunken or are sinking into the sea, exposing their terrestrial erosion pattern to surf activity (Valentin 1952). They are characterized by steep slopes, bending and winding outlines, and generally rocky shores (for example, the Aegean or Dalmatian coasts). With ageing, coasts begin to accumulate coarse sand in sheltered bays, and their outlines become more and more straight until in old age straight coastlines with long, lined up sandy beaches are dominant, as on the east coast from Long Island southward.

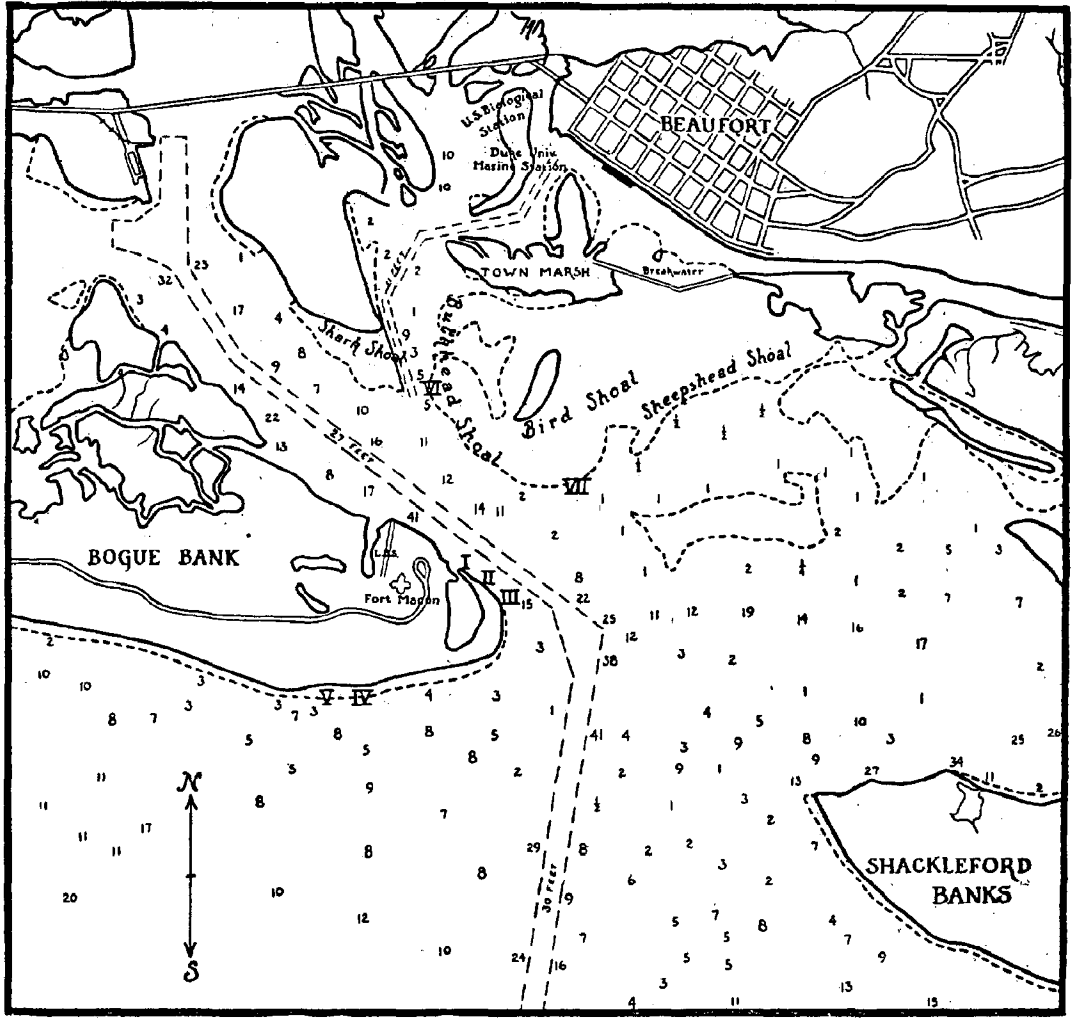
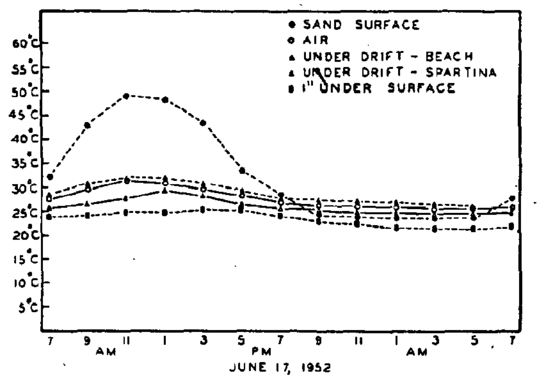
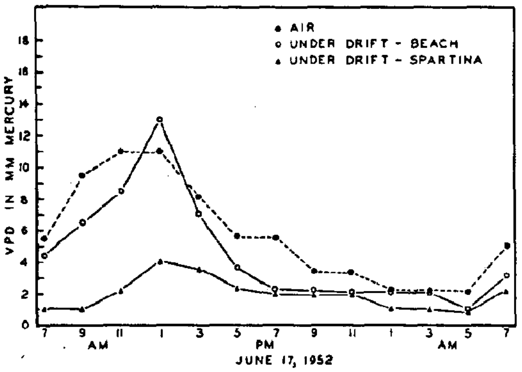

BEAUFORT
U.S. Biological Station
Duke Univ. Marine Station
TOWN MARSH
Breakwater
Shark Shoal
Bird Shoal
Sheepshead Shoal
27 Feet
30 Feet
BOGUE BANK
L.S.S.
Fort Macon
SHACKLEFORD BANKS
I
II
III
IV
V
VI
VII
N
S

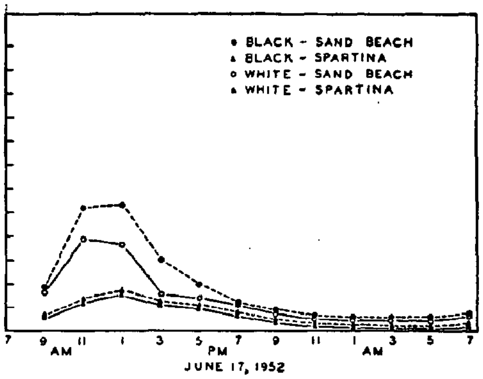
Fig. 10: Map of Beaufort Harbor, North Carolina. Water depths are given in feet (From Pearse, Humm, and Wharton 1942; Fig. 1).



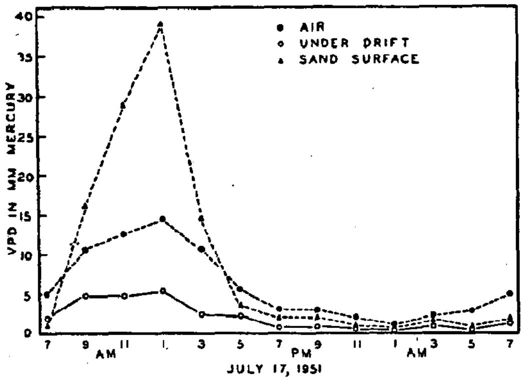
Temperature variations on Piver's Island on a summer day



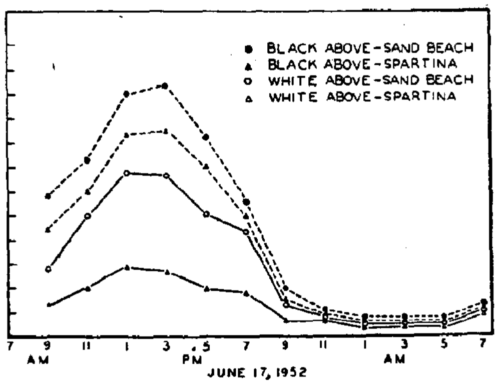
Variations in vapor pressure deficit on Piver's Island on a summer day.



Evaporation rates under the drift on Piver's Island on a summer day.



Variations in vapor pressure deficit on Piver's Island on a summer day.



Evaporation rates over the drift on Piver's Island on a summer day.

Fig. 11: Graphs showing diurnal variations in temperature, vapor pressure deficit, and evaporation for air, sand surface, and over and under drift on Pivers Island beaches (Beaufort, N.C.) on a summer day (From Barnes and Barnes 1954; Figs 3, 4, 5, 6, 7).

Fig. 12: Comparison of the activity of the spider population beneath and outside of the drift during day and night on Pivers Island (Beaufort, N.C.) (From Barnes and Barnes 1954; Fig. 13).

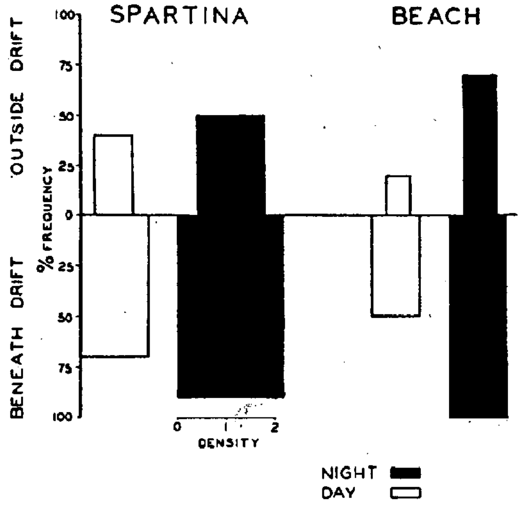


Fig. 13: Carapace length frequency of the mole crab, Emerita talpoida collected during the summer of 1940 at Beaufort, N.C. (From Pearse, Humm, and Wharton 1942; Fig. 18).

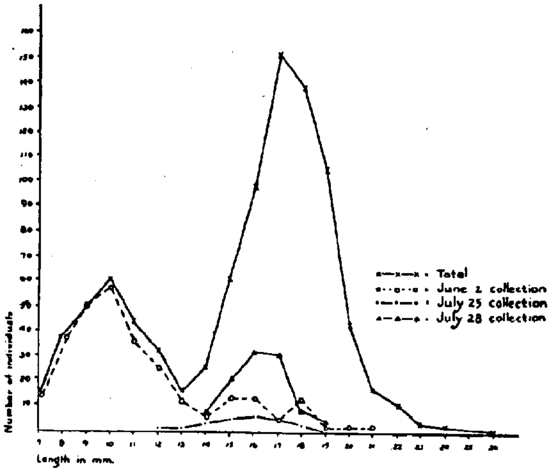


Table 5: Results of collecting on sand beaches at Beaufort, N.C.
(From Pearse, Humm, and Wharton 1942; Tables 6 and 7).

68 Seine Hauls
(Summer 1939, 1941)

Place	Ft. Macon, Outside				Ft. Macon, Inside				Bird and Sheepshead Shoals			
No. of hauls	10		16		3		18		6		15	
Summer	1939		1941		1939		1941		1939		1941	
Frequency	No. Times	Ave. No.	No. Times	Ave. No.	No. Times	Ave. No.	No. Times	Ave. No.	No. Times	Ave. No.	No. Times	Ave. No.
Silverside *Menidia menidia*	10	112.7	12	18.1	2	56.0	8	4.0	6	24.5	10	116.8
Anchovy *Anchioviella mitchilli*	7	31.7	1	0.3	1	50.2	..	....	..	....	2	0.3
Killifish *Fundulus majalis*	1	0.5	5	4.3	1	1.3	5	2.1	3	13.5	6	41.2
Pompano *Trachinotus carolinus*	8	11.4	4	2.3	..	....	2	0.3	..	....	..	....
Pinfish *Lagodon rhomboides*	2	0.2	..	....	1	0.7	3	3.2	..	....	2	0.3
Lizard Fish *Snyodus faetens*	..	....	..	....	3	2.7	1	0.1	1	0.2	1	0.1
Blue Crab *Callinectes sapidus*	2	0.3	7	3.4	..	....	6	2.0	3	0.7	11	2.5
Northern Kingfish *Menticirrhus saxatilis*	6	4.2	5	1.4	1	0.3	..	....	1	0.2	1	0.1
Flounder *Paralichthys dentatus*	2	0.2	2	0.2	..	....	4	0.5	2	0.5	5	0.3
Flounder *Paralichthys albiguttulus*	..	....	..	....	2	0.7	..	....	..	....	..	....
Portunid Crab *Aranaeus cribrarius*	5	0.5	10	5.1	..	....	..	....	1	0.2	1	0.1
Croaker *Micropogon undulatus*	..	....	6	1.4	..	....	4	3.4	..	....	..	....
Mole "Crab" *Emerita talpoida*	1	0.7	3	1.1	1	0.3	6	1.0	..	....	..	....
Hermit Crab *Pagurus longicarpus*	..	....	3	0.3	..	....	2	0.2	1	0.5	6	2.4
Jack *Caranx hippos*	..	....	3	0.5	..	....	..	....	..	....	1	0.5
Mullet *Mugil cephalus*	..	....	1	0.2	..	....	6	4.0	..	....	..	....
Spot *Leiostomus xanthurus*	..	....	2	1.0	..	....	4	1.8	..	....	1	0.1
Pipefish *Syngnathus fuscus*	..	....	2	0.2	..	....	2	0.1	..	....	..	....
Lady Crab *Ovalipes ocellatus*	..	....	2	0.3	..	....	3	0.4	..	....	..	....
Triggerfish *Balistes carolinensis*	..	....	2	0.1	..	....	3	0.4	..	....	..	....
Snail *Terebra dislocata*	..	....	..	....	..	....	1	0.1	1	0.2	..	....
Beach Clam *Donax variabilis*	..	....	3	0.9	..	....	..	....	1	0.2	..	....
Ascidian *Styela partita*	..	....	..	....	1	0.3	..	....	1	0.2	..	....
Ctenophore *Mnemiopsis leidyi*	1	0.1	..	....	..	....	..	....	4	18.3	..	....

Rake Net Catches
(Summer 1941)

Locality	Ft. Macon, Outside		Ft. Macon, Inside		Bird and Sheepshead Shoals	
No. of hauls	21		20		21	
	No. times	Ave.	No. times	Ave.	No. times	Ave.
Portunid Crab *Arenaeus cribrarius*	7	2.4	1	0.1	..	...
Sand Dollar *Mellita quinquiesperforata*	..	...	..	...	10	8.2
Blue Crab *Callinectes sapidus*	3	0.5	3	0.3	3	0.2
Lady Crab *Ovalipes ocellatus*	2	0.1	3	0.2	2	0.1
Mole Crab *Emerita talpoida*	1	0.1	2	0.1	..	...
Portunid Crab *Callinectes ornatus*	1	0.1	..	...	1	0.1
Hermit Crab *Pagurus longicarpus*	3	0.3	..	...	12	2.3
Flounder *Paralichthys dentatus*	..	...	2	0.1	4	0.3

Table 6: Lengths of shells (in millimeters) of common molluscs on Fort Macon beaches (Beaufort, N.C.) (From Pearse, Humm, and Wharton 1942; Tables 9 and 10).

Olivella mutica

(Picked up by hand)

Locality	Date	No. exam.	Max.	Min.	Ave.
Sheepshead Shoal.....	June 20	76	15.0	4.6	8.9
Sheepshead Shoal.....	July 2	51	13.0	5.0	8.5
Sheepshead Shoal.....	July 4	94	12.2	4.7	8.9
Sheepshead Shoal.....	July 8	43	13.0	4.3	8.9
Shackleford Bank.....	Aug. 7	30	11.0	2.4	7.9
Ft. Macon Beach, inside.....	Dec. 7	5	7.4	6.1	6.9

Donax variabilis

(Sifted from sand)

Date	No. exam.	Max.	Min.	Ave.
June 17.....	1090	9.5	2.1	4.8
July 19.....	224	13.0	3.0	5.8
July 21.....	164	12.5	2.3	7.6
Sept. 10.....	103	10.0	2.5	5.4
Dec. 7.....	71	9.0	4.1	5.7

Table 7: Seasonal changes in condition of female Emeritas collected on beaches at Beaufort, N.C. (From Pearse, Humm, and Wharton 1942; Table 11).

Date	No. with eggs	No. with small males	Total
1940			
June 2.....	43	0	292
July 25.....	22	0	25
July 28.....	103	0	104
July 29.....	13	0	13
August 3.....	12	3	16
August 7.....	25	11	37
August 16.....	61	34	97
August 18.....	76	24	105
August 20.....	38	46	88
August 24.....	7	22	32
August 27.....	25	27	53
August 30.....	14	38	53
December	0	0	7
1941			
June 28.....	33	0	54
December 7.....	0	0	17

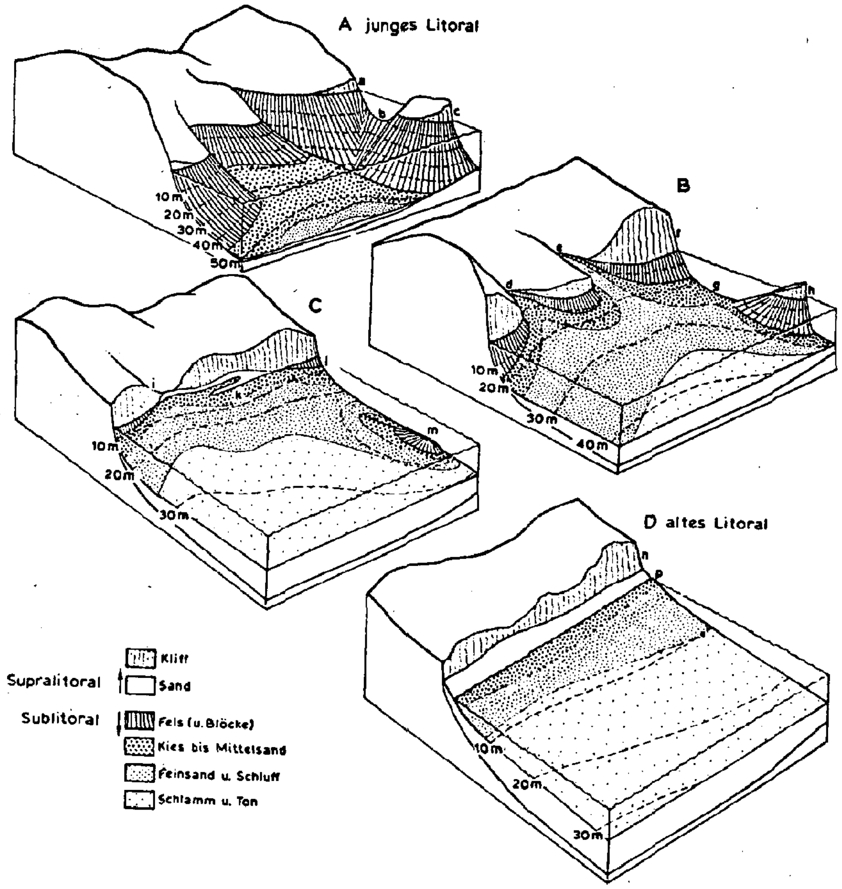

A junges Litoral
a
b
c
10m
20m
30m
40m
50m
B
d
e
f
g
h
10m
20m
30m
40m
C
i
k
l
m
10m
20m
30m
D altes Litoral
n
p
10m
20m
30m
Kliff
Supralitoral
Sand
Sublitoral
Fels (u. Blöcke)
Kies bis Mittelsand
Feinsand u. Schluff
Schlamm u. Ton

Fig. 14: Diagram of changes in the coastal environment during ageing of a coast (A-D). A newly-formed cliff; b. submerged rock; c. island; d. shingle; e. sandy bay; f. high cliff; g. saddle connecting submerged mountains; h. crag; i. rudimentary sand beach; k. sand bank; l. disappearing rocky littoral; m. submarine mount; n. unbroken cliff line; p. unbroken beach (From Riedl 1966; Fig. 316).

High energy beaches vary enormously in their dimensions. The youngest beaches, mainly at the ends of bays in young shorelines, are only a few meters long and broad. They consist of a coarse sand layer, just a few centimeters thick, which overlies the rocky surface. Old beaches may reach an unbroken length of a thousand miles and a breadth of several miles, particularly when the vertical coastal angle (between surface and coastal inclination) is small and an open ocean basin provides long fetch with long swells. The thickness of the sediment bank underneath the shore (Fig. 15) may reach 8000 feet, as measured between New York and Norfolk, and during the time this layer was piled up, the beach presumably moved 100 km toward the sea.

Interstitial space between sand grains is an important aspect of high energy beach systems, and continual sorting due to wave forces prevents it from being infiltrated by finer sediments. Consequently the substratum, although in perpetual motion, is a permanently porous system. In areas of high sediment deposition, however, primary beaches often are cut off from surf stress by the piling up of new offshore banks which build long islands and embay the older primary coastline in sheltered sounds (See Fig. 10). These older coastlines then accumulate fine sediments and turn into mudflats and marshes. Yet as they lose their sandy character, the new high energy beach at the front of the offshore bank develops. The sounds gradually fill through deposition, but although the land area increases, the biological continuity of the beach system remains unbroken.

The continuous balance between movement of its particles and stability of its entity is characteristic of a sandy beach. Reduction of mobility destroys the system, as does instability. The system's balance is due to a self-designing interaction between coastal inclination, sand grain sorting, and erosion-transportation-sedimentation relationships.

Geomorphology

The geomorphological pattern of a sand beach consists of fringing barriers and troughs offshore, a surf slope, and surf terraces whose dimensions vary with local tides and wave force. It also includes an extension (underneath coastal dunes) into the coastal groundwater system.

A cross section of a beach (Fig. 16) shows a series of steps and terraces within three main regions. In the offshore region, bars and troughs are lined up parallel to the coast. These bars, mostly from one to a few feet high, usually remain below water. In some areas they pile up to the low tide level, reaching several miles in length and several hundred yards in breadth (known as "Sande" in the North Sea). In high sediment areas, as already mentioned, they may rise above sea level as fringing offshore banks. They may line the coast, producing long bays and cutting off former high energy beaches from surf stress (locally known as outer banks, "Haff" or "Lido", and as sounds, "Neerung" or "Laguna").

The foreshore region often includes several steps or levels varying with the local tidal dimensions and exposure. In going from sea to land, a low water step with shell and coarser sand and wells of brackish water is encountered, followed by a low tide terrace, characterized by coarse shell

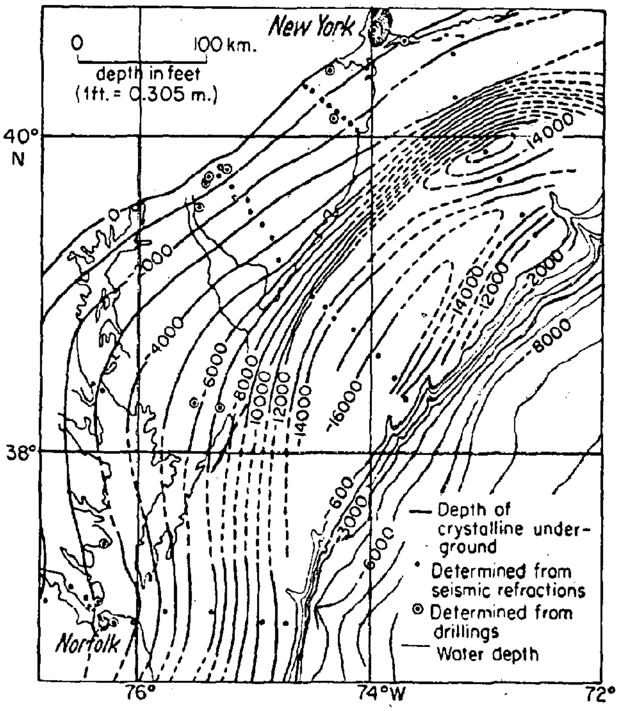

New York
0
100 km.
depth in feet
(1ft. = 0.305 m.)
40° N
38°
76°
74°W
72°
Norfolk
0
2000
4000
6000
8000
10000
12000
14000
16000
600
3000
6000
— Depth of crystalline underground
• Determined from seismic refractions
⊙ Determined from drillings
— Water depth

Fig. 15: Thickness of sedimentary banks in the coastal shelf area between New York and Norfolk (After Ewing, from Dietrich 1963; Fig. 13).

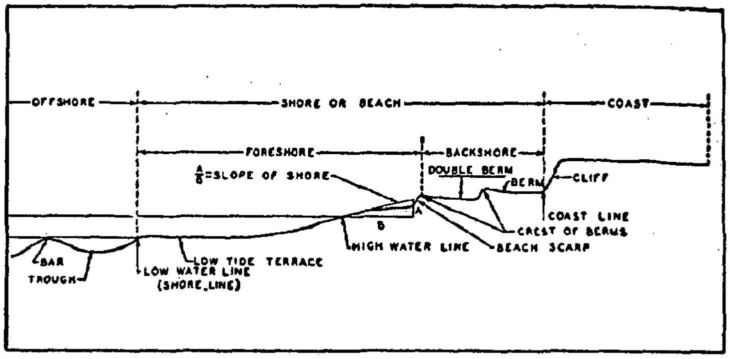

OFFSHORE
SHORE OR BEACH
COAST
FORESHORE
BACKSHORE
A/B = SLOPE OF SHORE
DOUBLE BERM
BERM
CLIFF
A
B
COAST LINE
CREST OF BERMS
BEACH SCARP
HIGH WATER LINE
LOW TIDE TERRACE
LOW WATER LINE (SHORE LINE)
BAR
TROUGH

Fig. 16: Terminology for a beach profile. Berms are small impermanent terraces formed by deposition during calm weather and by erosion during storms (After Shepard, from Kuenen 1950; Fig. 121).

particles, short ripple-marks, and flat ponds at low tide. Next is the high water step, sometimes clearly marked by long and dense stripes of finer shell. Next is the high tide terrace, characteristically smoothed by the tips of high water waves. Its upper limit is called the berm (Fig. 16).

At the first crest of the berm the foreshore region turns into the backshore region, which may consist of several sharply edged berms, surfaced with dry sand which end at the foot of a cliff or the first dune with some vegetation.

From a vertical view, the offshore bars show outlets kept open by a strong back or over flow, and the shoreline is serrated within several scales. On a small (1 to 10 m) scale are the beach cusps, sequences of flat embayments, with corresponding shallow submarine deltas as mirror images (Fig. 17). On a larger scale, beaches with stronger surf and landward currents show rip currents (Fig. 18) (Shepard 1948, Shepard and Inman 1950). These back currents locally form strong flows up to 1m/sec, reaching to 300 m off shore. In forming flat caps and deep feeder and neck channels, they carry finer sand far out to deeper waters. These phenomena participate in permanent sorting of the sediment as well as in the dynamics of beach development.

Finally, on a microgeological scale, ripple marks are both characteristic and important for high energy beaches. As a result of certain (not yet clearly understood) relationships between the speed of water particles and the length and rhythm of wave oscillation, ripples are formed (Fig. 19). They vary from 1 to 50 cm in wavelength, and their height varies between one-third and one-tenth of the length. In shovelling the sand into long crests, in changing their position and wavelength with every change in water movement, they contribute strongly to a permanent shifting and sorting in the surface layers.

Sedimentology

Sedimentology is a master key to differentiation in the interstitial environment. Much is clarified by simple grandulometrical investigations. However, the problems of hydrodynamics within a porous body is rather complicated. The importance of the edaphic structure (or substrate composition) is based on the fact that it permits prediction of three types of correlations: first, the outer or primary hydrodynamic conditions; second, the inner or secondary hydrodynamics within the sediment body; and third (in a preliminary way), the composition of the fauna selected.

The following six sediment parameters, in order of their general importance, are of biological significance. (1) The medium grain size (from 0.1 to 4.0 mm mostly) which is correlated with primary input of hydrodynamic energy. Mean grain size increases with energy and influences the absolute pore size, the maxima of interstitial currents, and the mobility of physical and organic components. (2) The grain size variation (σ), expressed in % of the main fraction, or in the number of peaks within the grain size curve. Low σ expresses high constancy of energy input, a maximum of relative pore volume and a uniformity of biological conditions. High σ, of course, shows the opposite. The number of peaks is an expression of the variation of energy input and the main features of the inner hydrodynamic and faunistic variability.

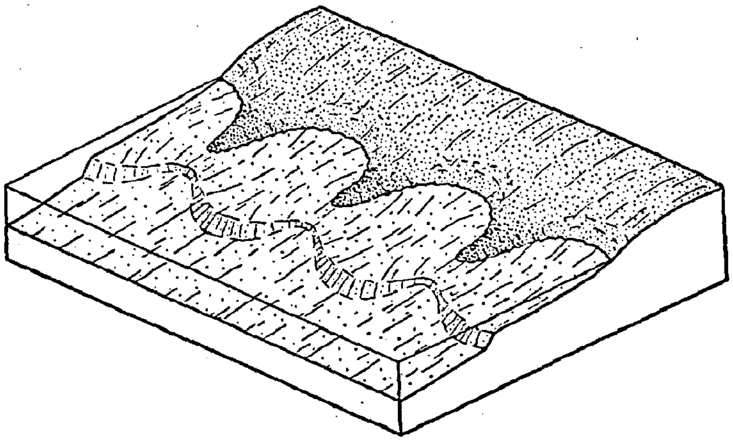


Fig. 17: Diagram of beach cusps, with submarine deltas corresponding to the embayments as mirror images (Mainly according to Timmermans, from Kuenen 1950; Fig. 130).

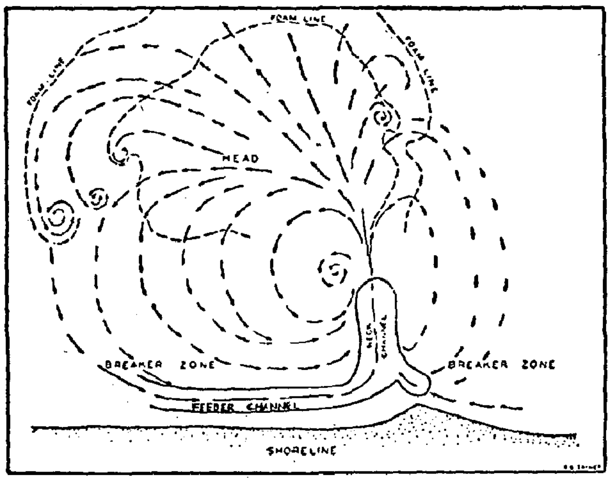

FOAM LINE
FOAM LINE
FOAM LINE
HEAD
NECK CHANNEL
BREAKER ZONE
BREAKER ZONE
FEEDER CHANNEL
SHORELINE

Fig. 18: Diagram of a rip current showing components and direction of net water movement. Relative velocity is indicated by length of arrows (After Shepard, from Kuenen 1950; Fig. 122).

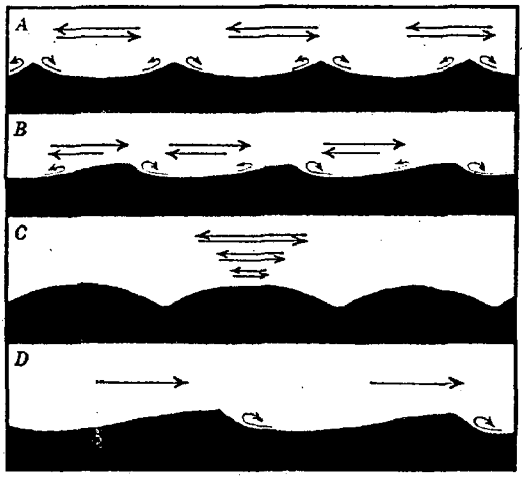


Fig. 19: Cross-sectional view of ripple marks. A. Symmetrical oscillation ripple marks; B. asymmetrical oscillation ripple marks; C. symmetrical oscillation ripple marks with rough troughs; D. current ripple (Kuenen 1950; Fig. 129).

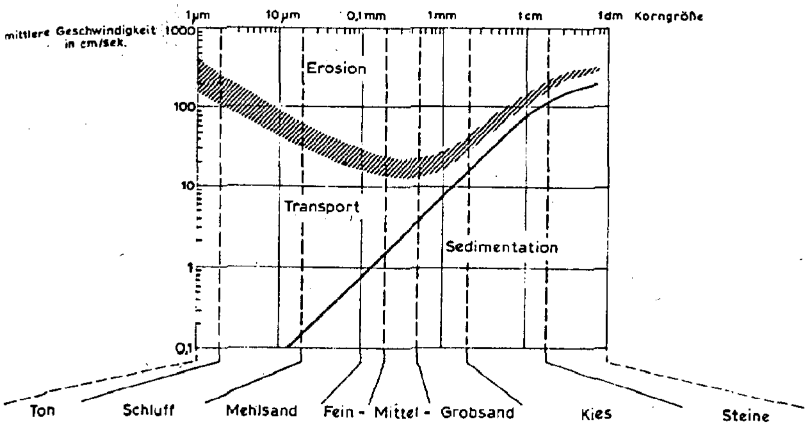


Fig. 20: Graph showing influence of particle velocity on the sorting of sediments. Cross hatching shows boundary between erosion and transport zones. Unbroken curve represents boundary between transportation and sedimentation zones (After Dietrich, from Riedl 1966; Fig. 314).

(3) The contributions of small-size fractions (expressed in % of fine sand, silt, and clay participation). Reflecting the extent of minimum periods of dynamic stress, these minimum fractions reduce dramatically the pore space in a relative as well as in an absolute sense. A small amount of fine sediment often chokes the whole pore system, cuts off ventilation and lifts the deep, anaerobic layer up to the surface (See Fig. 51) (Brafield 1964).
(4) The amount of decomposable organic matter in the sand (given in % of carbon times 1.8 and in % of nitrogen times 18, or in measurement of deterioration of the climate gives a general idea of the input-consumption relationship. This, of course, is of high importance, although methodology and interpretation of data are still creating arguments. Generally speaking, the average of around 1% decomposable organic matter decreases with grain size and with distance from the coast (grain size generally decreases with increasing coastal distance). Although the organic amount can reach high percentages (if an organic wrag bed becomes imbeded within sediment layers), under high dynamic input it remains remarkably low. Yet, the amount of food available in a given time not only depends on the storage, but even more on the speed with which nutrients are deposited and decomposed within the system. It is clear that higher hydrodynamic energies, larger pore space and higher flow-through rates provide chances for speedier energetic loops.

(5) Form and packing of the sediment particles (defined as edged to rounded, and loose to tight) again are correlated with hydrodynamic energies and have strong influence on the pore system. Roundish forms show grinding, and result from packing and shaking activity. Computation of pore space in loosely packed as compared with tightly packed spherical grains (of equal size to make it simple) is based on the relation of the volume of a cube (as opposed to that of a pentagonal dodecaeder) to the volume of its inscribed sphere.

(6) Finally, the amount of calcarous matter (in %) demonstrates the origin of the sediment. Higher percentages probably offer a buffering system in cases of low pH.

Besides these general characteristics of sand composition there is also a rather complicated and dynamic pattern of their interaction. This pattern is three dimensional, varying from capes to bays, with distance from the surf zone, and from the surface to the deeper layers. In sand environments it is characteristic that all these gradients dynamically change with each change in the hydrodynamic forces.

Hydrodynamic conditions must be balanced between erosion, including sorting, and deposition effects. If erosion overbalances sedimentation, the beach disappears. If deposition predominates over sorting and erosion the interstitial space is soon filled and the beach becomes a mud flat. The erosion of silt requires water movement at a rate of about 80 cm/sec (Fig. 20), while medium sand (0.2 - 0.5 mm) loses stability in water moving at the rate of 20 cm/sec. In other words, sand is eroded much more readily than clay. The opposite is true with regard to rate of sedimentation. Sand settles out at a water speed of only 10 cm/sec while clay remains in suspension until water flow rate is reduced to 0.1 cm/sec or less.

The self-balancing effect between erosion and deposition involves four factors: the boundary effect, friction, critical depth, and coastal angle. The boundary layer effect (Fig. 21) is partially responsible for the relative resistivity of fine sediment to erosion. Currents (of liquids or gases) are drastically reduced in speed as they approach solid surfaces, due to friction with these surfaces, and turbulent particle movement becomes laminar. Boundary layer dimensions along coastlines depend on viscosity of the water, roughness of the bottom surface, and speed, length, and duration of the current, but lies between a few millimeters and a few centimeters. Larger sediment particles, therefore, are reached by currents of greater speed, while finer particles are relatively protected.

Seas with wave heights of one to two meters and a period of 4 to 6 seconds have a particle speed of 80 to 100 cm/sec; a speed of 60 to 80 cm/sec reaches the coast. Both sand and silt go into suspension, but with increasing depth (Fig. 22) the orbital movement of the rotating or oscillating water particles is reduced by friction. At 10 to 20 m depths particle speeds of 10 cm/sec are reached, and all sand settles out and is trapped at the coast. Clay, however, remains in suspension and is transported far offshore and down the edge of the continental slope.

The permanent balance between erosion, transport, and sedimentation not only guarantees the preservation of the sandy beach environment but also causes high structural diversity. Geologically the result is described as false bedding, current bedding, and cross bedding. Biologically drastic changes and inversions of the common faunal gradients result. Coarse shell with low organic load, having attracted a brackish groundwater drain, may be covered by strongly reduced fine sediment with high organic content, and so on.

Another sand trap within the self design of high energy beaches is based on the laws of critical depth. Seas start to "feel" the bottom at a depth corresponding to wave length (Sverdrup, Johnson, and Fleming 1942). The oscillation space of the orbital movement of waves becomes narrowed, making the seas slower and steeper, and bending the wave crests toward the beach front. At a depth of about a half wave length the energy input toward the bottom becomes biologically important. This outer boundary of reduced oscillation space is called the second critical depth and lies at 100 m (Figs. 22 and 23). In this oscillating body of water sandy bottoms appear, characterized by rigorous sorting, removal of fine sediments, and formation of long ripple marks. The upper limit of marine sand biota depends on tide dimension and local wave energies. It often reaches 4 and sometimes 8 m above midwater level.

Within the reduced oscillation space and with decreasing depth the speed of the waves decreases and their height increases until the front of the seas becomes too steep for harmonious oscillation, and breakers are formed. This happens at a depth which corresponds to about 2.5 times wave height, the first critical depth (Figs. 22 and 23). In the breaker zone a remarkable amount of wave energy is consumed in counteraction of turbulent water forces. Not the original forces but "residual waves" (translation waves) finally reach the land. The amount of energy reaching the surf slope and the surf terraces, however, depends on the vertical coastal angle. The steeper it is, the nearer is the first critical depth to the waterline and the greater is the proportion of the

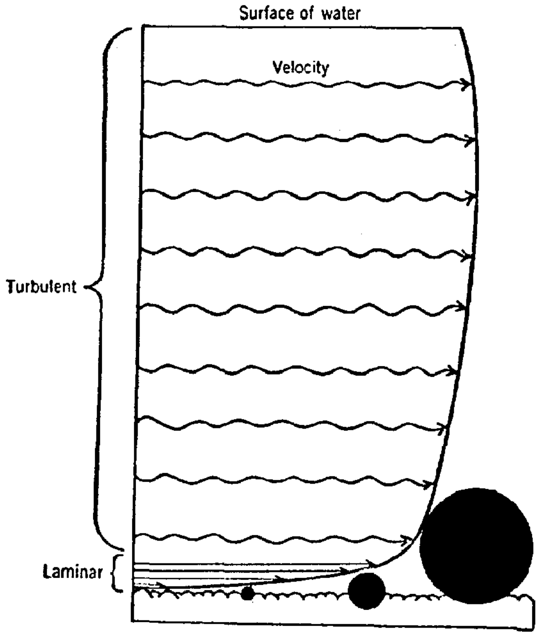


Fig. 21: Schematic section of a current, showing distribution of velocity and turbulence. The boundary layer is represented by the straight arrow region. Larger particles on the bottom are influenced by greater velocity than small particles (From Kuenen 1950; Fig. 117).

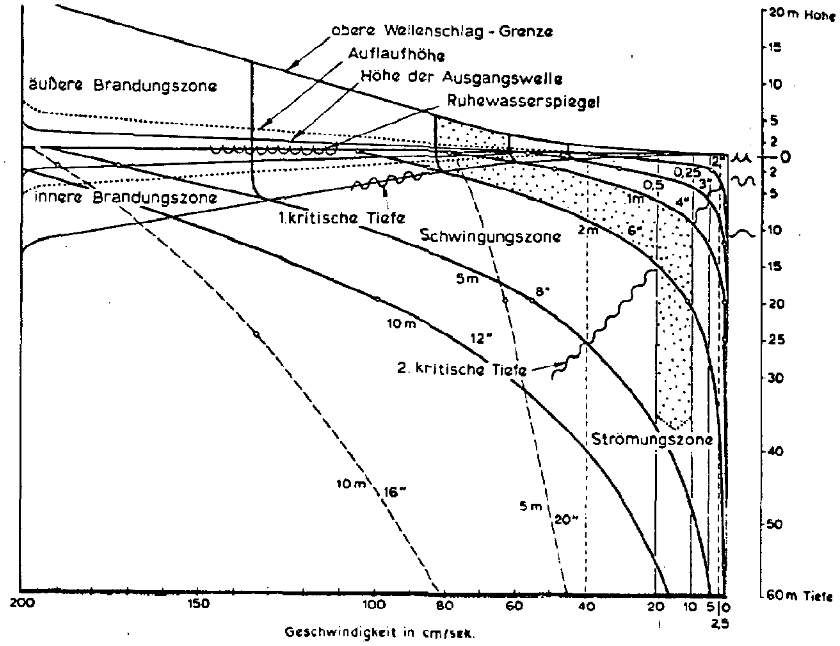


Fig. 22: Graph showing decrease in particle velocity in the sublittoral according to wave action and current. The coordinates are particle speed and depth. Solid lines show speed reduction (cm/sec) with increase in wave height (m). Stippled area shows the average condition (From Riedl 1966; Fig. 317).

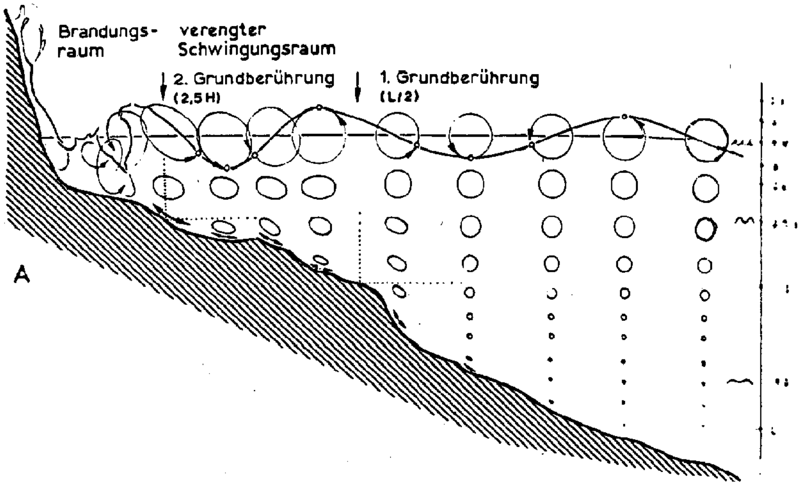

Brandungs-
raum
verengter
Schwingungsraum
2. Grundberührung
(2,5H)
1. Grundberührung
(L/2)
A

Fig. 23A: Diagram showing transformation of the orbital movement of particles with respect to depth and distance from the bottom. The two arrows indicate critical depths: first critical depth at 2.5 wave height and second critical depth at 1/2 wave height (From Riedl 1966; Fig. 212).

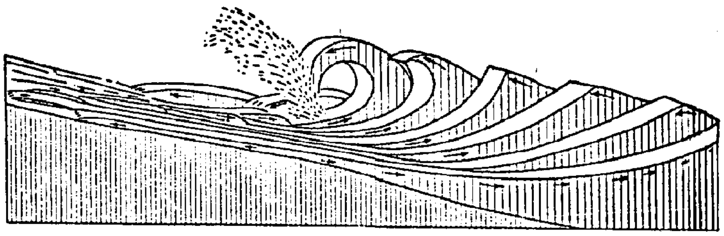


Fig. 23B: Diagram showing energy consumption in the breaker zone (After Davis, from Kuenen 1950; Fig. 54).

original forces that reach the beach. If, now, erosion at the water's edge occurs, sand is displaced there, but deposition increases in the outer oscillation zone, the vertical coastal angle decreases, the second critical depth moves farther offshore, the residual waves lose energy, and the system becomes balanced again.

If particle speed during the maxima of local surf beat reaches 100 cm/sec all sand fractions go into suspension. A drop to 50 cm/sec immediately releases gravel, and a drop to 20 cm/sec releases coarse sand. Finer fractions settle out at speeds between 5 and 1 cm/sec, contributing to further decrease in vertical coastal angle. On the other hand, high local particle speeds erode deep bays in the beach front. The deeper they are, the smaller the horizontal coastal angle becomes (angle of open sea, seen from a point at the shore), and the smaller are the chances of being reached by seas from many directions. As the exposure index decreases, so does the vertical coastal angle. The opposite is true for sheltered bays. They soon fill in and are incorporated into straight beach fronts. Extremely long, smoothly bending beach lines are the result of the continued action of these self designing mechanisms.

Amount of sediment production and distance of sediment transport are also important for beach formation. There are four major sources of sediment: rocky shores, benthos communities, landslides, and plankton communities; and three major types of sediment: boulders (or cobble), sands, and clays (Fig. 24A). Erosion on rocky shores produces mainly boulders, cobble, and gravel, but sand is also produced in fair amounts. Greater contributions to beaches are made by calcareous benthic biota: shell beds and algal and coral reefs. The participation of boring animals and the chewing activity of errant benthic macrofauna can be enormous in the decomposition of reefs and in grinding shell and coarse sand fractions into finer sands. Plankton shells produce mainly oozy fractions without much additional erosion. Terrestrial erosion, transported mainly by rivers but partly by storms, contributes mostly sandy fractions, but also clay.

In a 10 m deep water body (average for a beach environment) coarse material, cobble and gravel settle in seconds (Fig. 24B) and are deposited near their source. Sand usually takes less than a minute (10 to 60 sec) and remains in the surf area. Because of the balance between erosion and deposition and the prevailing currents parallel to the coast, sand is shifted along the shoreline. Silt and clay require from an hour up to 1.5 months to settle in the same 10 m, and may be transported very far into deeper waters.

Sediment derived from the land decreases from large continents to small oceanic islands, but reefs and calcareous benthic communities increase from cold to tropical waters. For these reasons, continental shores in cold-temperate climates contain only quartz grains while tropical waters are surrounded by fairly pure calcareous sands.

In more stable situations the contribution of the macrofauna to sand structure becomes observable (Fig. 25). The "rake structures" ("Wuhlgefuge", Schaefer 1962) of raking and digging animals are very specific, and when in large numbers these animals strongly influence a layered substratum. Further-

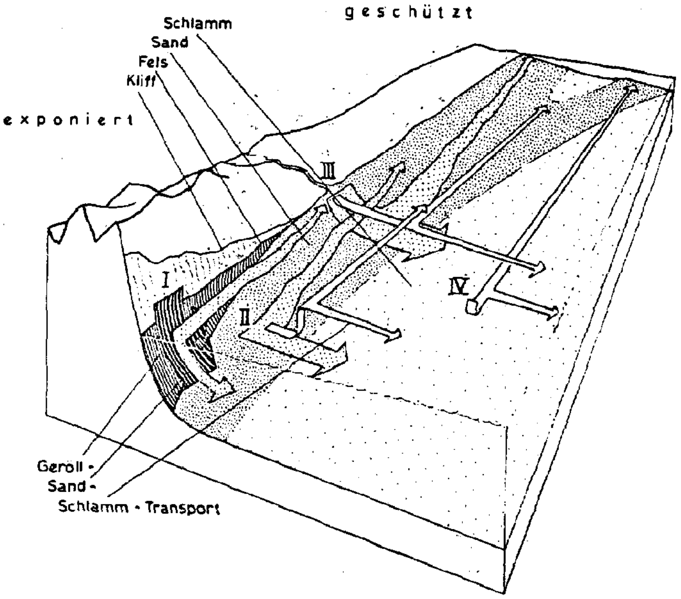

geschützt
exponiert
Schlamm
Sand
Fels
Kliff
I
II
III
IV
Geröll -
Sand -
Schlamm - Transport

Fig. 24A: Diagram of sediment production and transportation. I. Shore contribution; II. benthos contribution; III land contribution; IV. plankton contribution. Striped arrows represent stone, stippled areas sand, and white arrows clay (From Riedl 1966; Fig. 315).

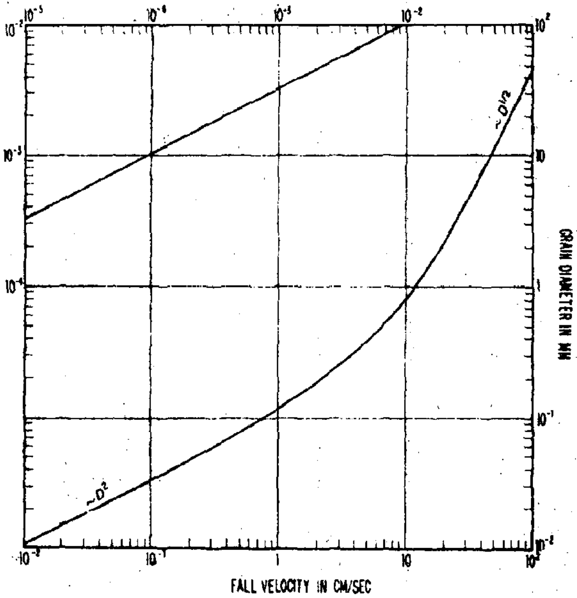


Fig. 24B: Graph showing fall velocity of quartz-density grains of average natural shape at 20°C (From Bagnold 1963; Fig. 1).

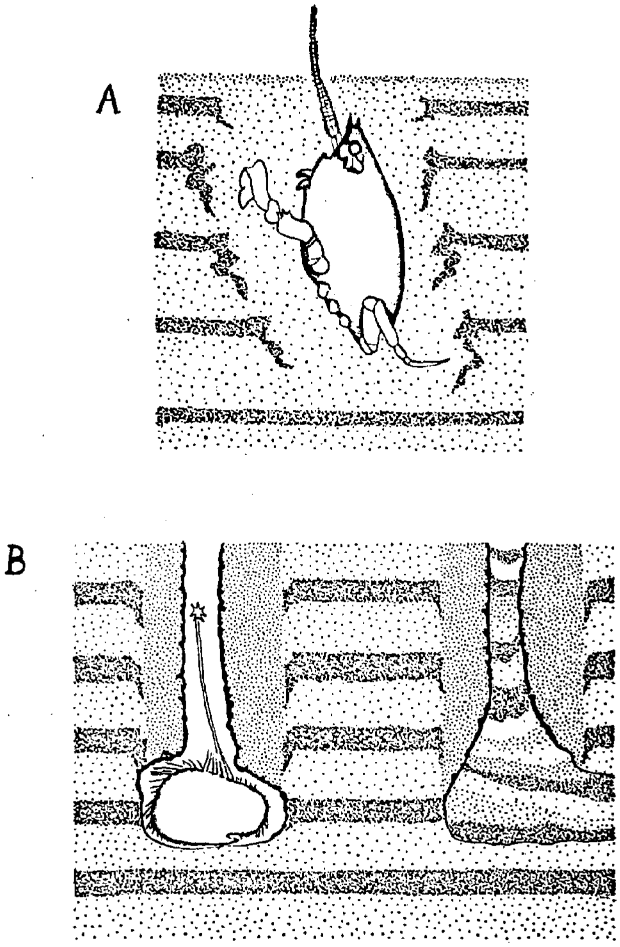


Fig. 25: Diagrams showing the influence of digging organisms on sediment layering. A. The small crab *Corystes*. B. The heart urchin *Echinocardium* (From Schaefer 1956; Fig. 16)

more, over long time periods the chewing of the sediments by many types of the macrofauna (the "organic mill") causes a decrease of grain size in deeper and older layers.

Highest particle mobility is demonstrated by coarse shell within the surf zone. During the incoming tide this material is collected and transported to the high tide mark. During outgoing tide it is washed back or remains partly scattered over the whole tidal zone. This happens so rhythmically, that, for some species of Turbellaria, it serves as a permanent lift, holding them in the high energy area (Rieger and Ott 1969). Lowest particle mobility is related to the deepest sand layers, where influence of terrestrial soil occurs, or the marine sediment itself turns into subfossil conditions.

Interstitial Climatology

Interstitial climatology offers both static and dynamic aspects. Since measuring currents in the pore space is still a problem, investigations of parastatic gradients have been preferred, and dynamic explanations have been generally derived. Eleven partly correlated parameters of interstitial climatology should be taken into consideration (Figs. 26 and 27). (1) Temperature strongly varies in surface layers, due to evaporation and to heat storage in dry sand under summer radiation. It is low and most stable in the groundwater horizon. (2) Water saturation changes between groundwater and surface levels. (3) The same is true for salinity, but there is also a gradient between the marine and the limnic groundwater, producing a zone of brackish water between. (4) Oxygen availability is relatively high in the moist supralittoral zone, but it drops drastically within the deeper layers. Hedgpeth (1957b) points out that "an almost universal characteristic of sandy beaches is the dark or black layer in the region of stagnation and oxygen deficiency resulting from the formation of ferrous sulfides under reducing or anaerobic conditions." The study of this anaerobic stratum, however, has only recently begun. Its depth beneath the surface is related both to wave action and to the interstitial space of the porous system and ranges from a few feet in coarse sand and shell subject to heavy surf to a few millimeters in more protected areas with mostly fine sand (See Fig. 51B). As Hedgpeth says, "Since the formation of ferrous sulfide in sand is a phenomenon of significance in general problems...it is unfortunate that it has not been studied in more detail". (See Bruce 1928b, Pennak 1951, Perkins 1957, Gordon 1960, Brafield 1964, Riedl 1969, Fenchel 1969). (5) Free CO_2 levels rise remarkably in some shore layers. (6) Water hardness has been observed to increase with distance from the coast, along with (7) a slight drop in pH. Less information is available with regard to (8) gradients of decomposable organic matter, but there is evidence enough to predict remarkably strong differences. (9) Redox potential and (10) H_2S concentration have been measured only very recently, since the deeper anaerobic layer has remained nearly untouched. (11) Light is very limited in its distribution within the sandy beach system. Although high energy beaches generally are subject to strong radiation, light is cut off completely within the first surface layer. The thickness of this layer varies with the transparency of the sand and decreases with grain size from a few centimeters to less than one millimeter.

Rhythmical variations in the pattern of these parameters are caused by tidal, circadian, and seasonal changes in the outer climate. Tides influence

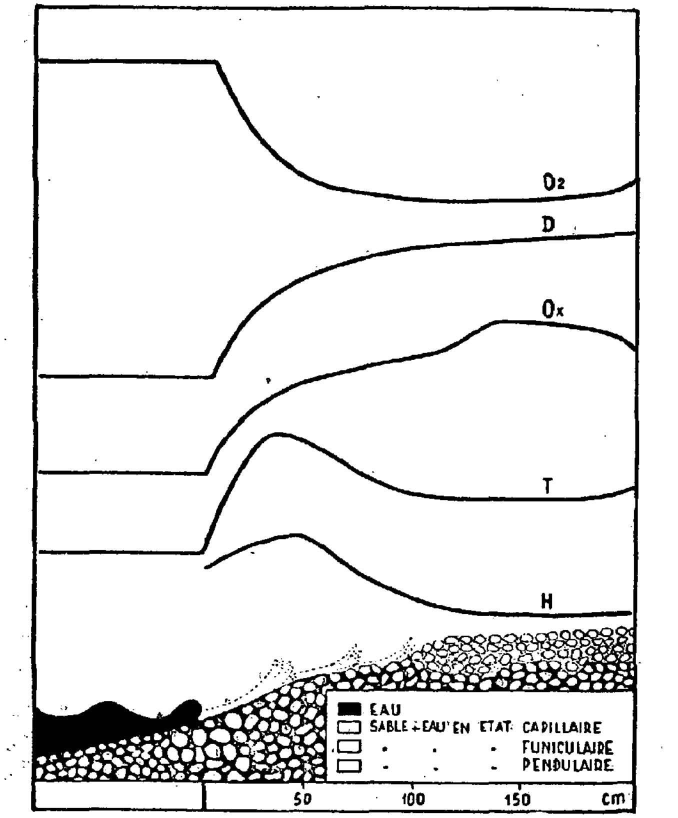

O2
D
Ox
T
H
EAU
SABLE + EAU EN ETAT CAPILLAIRE
FUNICULAIRE
PENDULAIRE
50
100
150
cm

Fig. 26: Diagram illustrating the changes in the physical parameters of interstitial water as a function of distance from the water's edge. H. Water content of interstitial space; T. temperature; Ox. oxygen deficiency; D. water hardness; O_2. Oxygen tension (From Delamare 1960; Fig. 24).

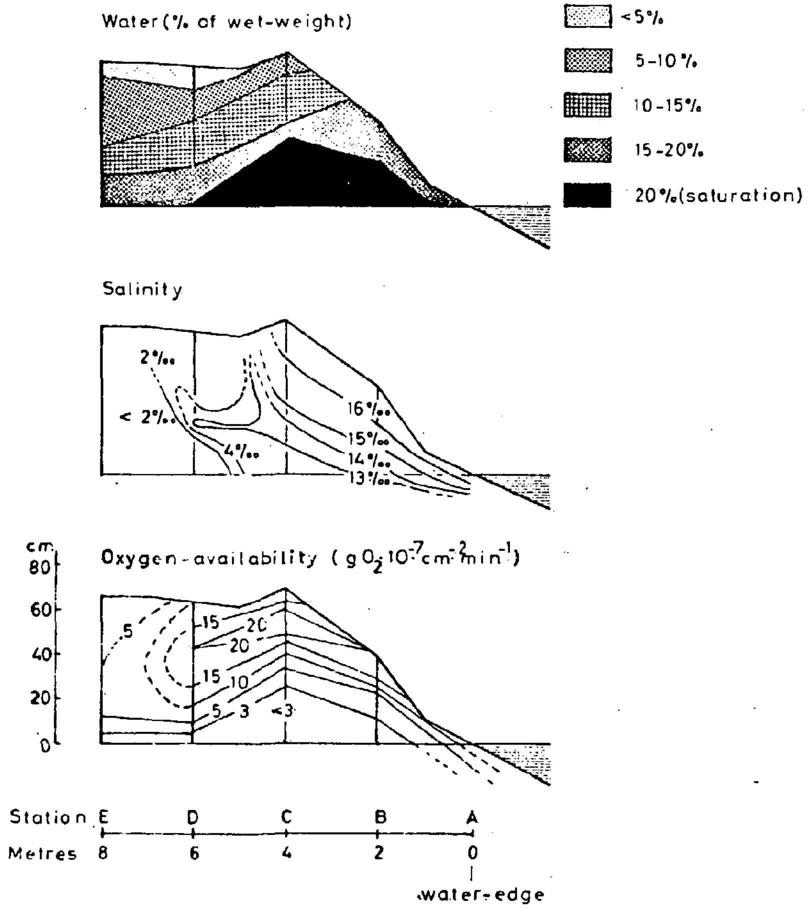


Fig. 27: Graphs showing distribution of pore water, salinity, and oxygen availability in Julebaek beach, August 23, 1967 (From Fenchel, Jansson, and von Thun 1967; Fig. 2).

the system by causing movement of the whole subcoastal water body governing most of the parameters. Circadian rhythms affect surface temperature and salinity mostly. Seasonal changes involve variation in radiation, precipitation, surface salinity, and temperature. They also influence the height of the ground water level and the position of the brackish water cushion.

The dynamics of the interstitial waters are to be understood in terms of three factors, all of which fill and drain the system in different rhythms. First, the sea between low tide mark and the first crest, with changing water levels and wave tongues acting at different heights. Second, evaporation and precipitation of marine spray or rain water over the whole surface. Third, seasonal changes in groundwater input from the land side, affecting the deeper layers. Five different water bodies can be differentiated in a complete high energy beach system (Fig. 28): a marine zone of permanent sediment displacement (transfer zone), a brackish mixing zone, a marine circulation zone, a moist sand (pecolation) zone, and a nearly fresh groundwater zone.

BIOLOGICAL ASPECTS

In physical respects sandy beaches have much in common with sandy deserts, yet their biota are very different. Until the 1920's the sand environment of the coast was considered to be the "marine desert" and remained biologically neglected until Remane (1933a) started investigations of the sandy coasts of Germany in the hope that the supposed impoverished biota there might offer fewer investigational difficulties than desert life. Since that time "psammology" or sand biology has become strongly developed, first in Europe and more recently in the United States. Today sand is known to be one of the richest and most challenging of marine environments, where thousands of highly adapted species have been discovered, where all invertebrate phyla are represented, and where the most unexpected problems concerning food sources, dynamics, and energy flows have arisen and are still largely unsolved.

Major Biota

The high energy beach system, as already mentioned, offers space for three main types of populations in contrast to most other biotopes which offer only two. In addition to providing space for epi- and endofauna (animals living on and in the substratum) porous systems give a third opportunity; space is also provided for a mesofauna living within the interstices.

The epipsammon

The epipsammon (Psammon, Greek for sand) contain species living on or above the sand surface. In a number of species, it is the least important link in these stratified groups. It contains a relatively small representation of the animal kingdom, but it is the only group which links marine and terrestrial species. Fishes and birds, as well as certain beetles, are in the group. The small representation is to be understood in terms of three facts: first, sand as a movable substratum is inhospitable to many types of organisms needing stable conditions or concealment; second, sand as a semi-liquid environment

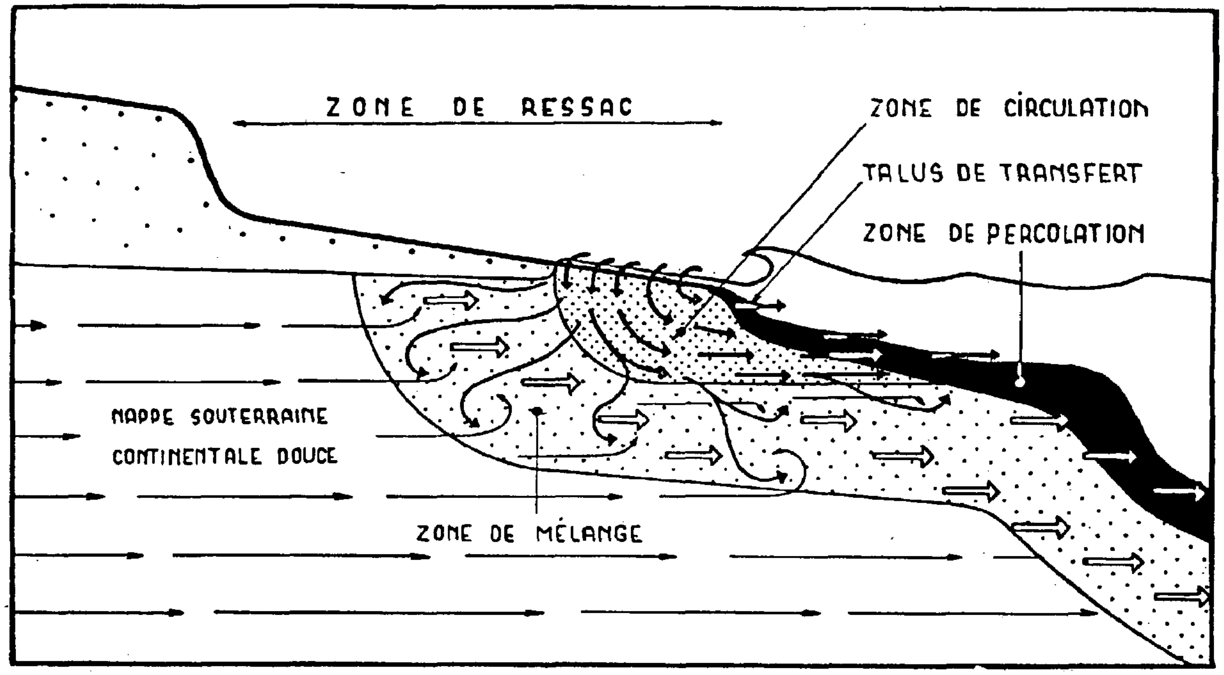

ZONE DE RESSAC
ZONE DE CIRCULATION
TALUS DE TRANSFERT
ZONE DE PERCOLATION
NAPPE SOUTERRAINE
CONTINENTALE DOUCE
ZONE DE MÉLANGE

Fig. 28: Diagram showing circulation of water in a sea without tides. Zone of Ressac is the foreshore area; closely stippled area is the circulation zone; black areas represent the transfer slope and zone of percolation; sparser stippling shows the mixing zone; long arrows indicate the subterranean continental groundwater area (From Delamare 1960; Fig. 6).

attracts endofaunal species of epifaunal origin which dig into the sand where they gain more stability as well as protection; third, it is usually the larger forms (macrofauna) that are strong and speedy enough to keep up with wave action (there is no foothold as on rocky shores for such animals as limpets, barnacles, or sea anemones), and these larger forms, the last link in the food chain, are always relatively few.

Although many fishes, birds, and beetles can be observed along shores (for example, 170 kinds of shore birds are listed for North America by Bent, 1927, 1929,) only a few are restricted to the high energy beach system. The sanderling (Crocethia alba) can be used as an example. This shore bird obtains "most of its food by probing in the wet sand...or by picking up what is washed up and left by the receding waves" (Bent 1927, 1929). Analogous fishes are representatives of Mullidae, probing the sand with their barbels. The tiger beetle (Cicindela dorsalis) can also be used as an example of organisms which are most often found on high energy beaches.

Adaptation to epipsammal life does not include obvious structural specialities, except barbels, and fish types bearing barbels are known from many different environments. Behavioral adaptations, on the other hand, are clear. Trophically, all types of epipsammon are animals adapted to collecting the endopsammon or their cadavers washed out of the sand or brought from the ocean, mainly in the meiofauna-size range (organisms of medium size).

The endopsammon

The endopsammon contain species which burrow in the sand but are too large to use the interstitial spaces (Fig. 2). This includes macro- and meiofauna. They build permanent burrows lined with stabilizing mixtures of secretion and fine sediment. When displaced, they hasten over the sand surface (cumaceans and many crabs) and disappear surprisingly quickly into the sand in a chosen place. In this respect they overlap with the epifauna. Members of the Rajidae, Soleidae and Uranoscopidae (rays, tonguefishes and stargazers) hide in the sand but feed on epipsammon macrofauna. Similarly, species such as mysids and male cumaceans rise at night to the surface but feed on bottom detritus or graze on sand grains. The endopsammon boundary can be drawn to include species, most of whose biological activities are restricted within the sand.

There is a much wider species representation in the endo- than in the epifauna, but it is far below that of the mesopsammon, especially on the high energy beach in its restricted sense. In locations of greatest wave stress, the endofauna is relatively limited to robust and quickly moving types (such as crabs); stationary or semi-sedentary types are absent. On the contrary, in more sheltered areas, stationary species (lancelets) or semisedentary types (seafeathers, sedentary polychaetes) are found. At least some of these types are not very sensitive to fine sediment accumulation. They even appear in biotopes where the interstitial space has vanished, leaving little in common with high energy beaches.

The representative endopsammon groups are mainly higher crustaceans; some molluscs and a few polychaetes and echinoderms are also typically represented. Among polychaetes, eunicids (Stauronereis), maldanids (Petaloproctus) and arenicolids (Arenicola) are represented, but mostly in extension of their main area on somewhat more sheltered shores. Of the amphipods, haustoriids (Haustoria) and talitrids (Orchestia, Talorchestia) may be abundant; among isopods, idotheids (Chiridotea) and among cumaceans, several families are common. Stomatopods are represented by Lysiosquilla. Decapods are more strongly represented. A few shrimps (Ogyris), thalassinids (Callianassa), albuneids (Lepidopa) and portunids (Arenarius), but particularly hippids (Emerita) and ghost crabs (Ocypode) are highly characteristic. Of the rest, some gastropods (Oliva, Terebra) are regularly present, and a few bivalves (Donax, Cardium) are typical of high energy beaches. Finally, among echinoderms, the sand dollar (Mellita) is a characteristic representative.

Adaptations are very distinct in several species, and their functions differ so greatly from those in the mesofauna, that they make differentiation between the two types reasonable.

Most striking are adaptations with respect to shape and locomotion in species living in the surf beat. Emerita disappears beneath the surface in a fraction of a second. Donax (even more surprising because a member of awkward bivalves) disappears in about a second. This unusual burrowing ability is due to adaptation of the legs in the first case (Fig. 29) and of the foot in the second. Coloration also can be an adaptation: the light sandy color without any pattern, as in the ghost crab (Ocypode), the beach "flea" (Talorchestia, an isopod), in Emerita, in Ogyris and others. Also eyes may be small (as in Emerita) and sensory bristles or tentacles very long and abundant (Pearse, Humm and Wharton 1942). During the breeding season, Emeritas have males attached to females and burrowing shrimp consort in pairs (See Table 7). This insures fertilization in the shifting environment.

Trophically the endopsammon do not contribute any primary producers to the system. No higher algae are represented in the high energy area, except for detached material stored as wrack beds on the shore, because of lack of substratum stability. The animals are mainly carnivores and herbivores. Some collect dead animals or feed in wracks, but even more important are the many types of suspension- or plankton-feeders. They range from hunter types, waiting in their burrows, through Emerita, filtering the back-flow of waves with its antennae, to highly specialized filter feeders such as lamellibranchs.

The mesopsammon

The mesopsammon have by far the greatest diversity of all psammon types, each beach system containing more than a thousand species, compared with several dozens in the epi- and endopsammon together. They also populate a three-dimensional environment, with microfauna having the greatest density (the macrofauna remain in surface contact and have a much lower density). Finally, the mesopsammon are highly sensitive to the slightest changes in edaphic conditions, which correspond exactly to differences in the overall hydrodynamic forces. Other psammobionts correspond in a much coarser fashion. Therefore psammologists often take only the mesopsammon into consideration when they talk about the sand biotope, and certain it is that mesopsammon are a most important and challenging subsystem. Faunal representation, adaptations, and trophic relationships will be analyzed.

Most surprising is the fact that representatives of nearly all main groups of the invertebrates have been able to adapt to the interstitial environ-

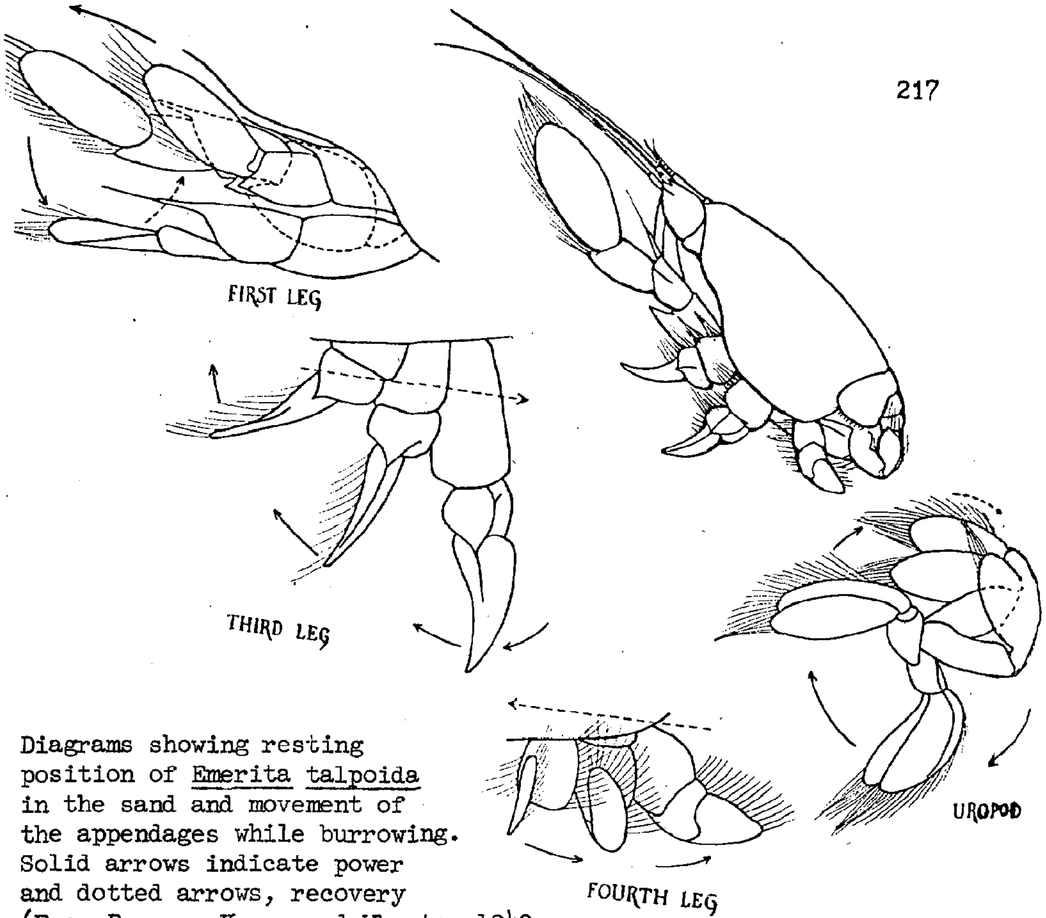

FIRST LEG
THIRD LEG
UROPOD
FOURTH LEG

Fig. 29: Diagrams showing resting position of Emerita talpoida in the sand and movement of the appendages while burrowing. Solid arrows indicate power and dotted arrows, recovery (From Pearse, Humm, and Wharton 1942; Fig. 22).

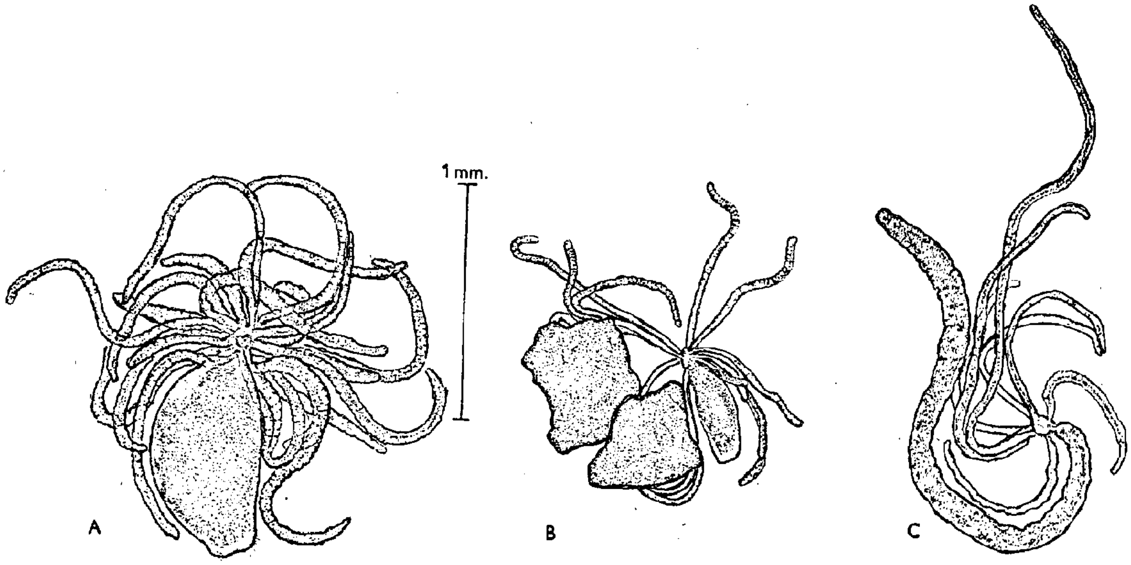


Fig. 30: Body shape in the genus Halammohydra. A. H. schulzei Remane; B. H. octopodides Remane; C. H. vermiformes Swedmark and Teissier (From Swedmark 1964; Fig. 3).

ment. Only a few groups have not: Porifera, Ctenophora, Scaphopoda, Cephalopoda, Decapoda, Hemichordata, all enchinoderms except holothurians, and finally Chaetognatha and Acrania. Problems of body structures, locomotion and trophic adaptation may have created insurmountable difficulties for these forms. However, interstitial ascidians and bryozoans, for example, have surmounted problems of body size as well as of locomotion in very unexpected ways, so representatives of some of these so far undiscovered groups may yet be found among the mesopsammon.

Among the many invertebrate groups represented, there are some nearly completely restricted to the interstitial environment. These are the phyla Gnathostomulida, Tardigrada and Gastrotricha, the orders and suborders Schizorhynchia, Archiannelida, Mystacocarida, Acochlidiacea and Actinulida and aberrant types of other groups such as the Madreporaria, Polychaeta, Bryozoa, Brachyopoda, Holothuroidea and Ascidiacea.

The systematic rank of restricted groups can be used as the measure of the age of their biotope. Without fossil documentation in a relative scale, we must assume that ancestors of systematic groups have to be stepwise older the higher their category in the classification hierarchy. Furthermore, we have evidence that larger groups have originated in their restricted environment (Riedl 1966). The very high rank of restricted psammon groups therefore lets us assume a very old age for the psammon biotope. As a matter of fact, only two other biotopes have restricted systematic groups of comparable rank: the pelagic and the pelos (muddy bottoms). Obviously, the sandy beach is one of the oldest biotopes on this planet.

The dominant groups in the mesopsammon are diatoms, ciliates, turbellarians, gnathostomulids, gastrotrichs, nematodes, and harpacticids (group of copepodes). The total groups represented number about twenty-three (a to w). Algae (a) are mainly represented by diatoms and bluegreen algae as well as by bacteria. Fungi (b) in the sand habitat have been described most recently (Kohlmeyer 1966). Protozoa (c) are very common, mainly long and slender ciliates as well as foraminifera attached in some cases to sand grains (Dragesco 1960, Rhumbler 1938). Coelenterates (d) are represented by several small, highly adapted groups, mostly belonging to class Hydrozoa with dwarf polyps or extremely reduced medusae, such as Othohydra, Halammohydra (Fig. 30), and Armorhydra; but microscopic representatives of classes Anthozoa and Scyphozoa have also been discovered. In the first case it is a bipolar madreporarian (Rossi 1961), in the latter a reduced stauromedusae (Salvini-Plawen 1966).

Turbellaria (e) are common, most typically represented by Otoplanidae (Ax 1956a, a group of Proseriata) and Schizorhynchia (Karling 1961, a group of Kalyptorhynchia). But also Acoela, Macrostomida, a new suborder of Catenulida (not yet published) and others are included. Gnathostomulida (f) a new phylum (Ax 1956b) is typical of mesopsammon, with more than 40 species and 10 genera already known (Fig. 31) (Sterrer 1968, Riedl 1969). Rotatoria (g) are less common but are represented (Remane 1933b). Gastrotricha (h) are extremely abundant members of the interstitial psammon, and in marine environments they are nearly restricted to sand. Considered earlier as aberrant types (Remane 1925), these strange forms (Fig. 32) are known today to constitute one of the main types in the sand environment (Wilke 1954). Nematodes (i) compose the

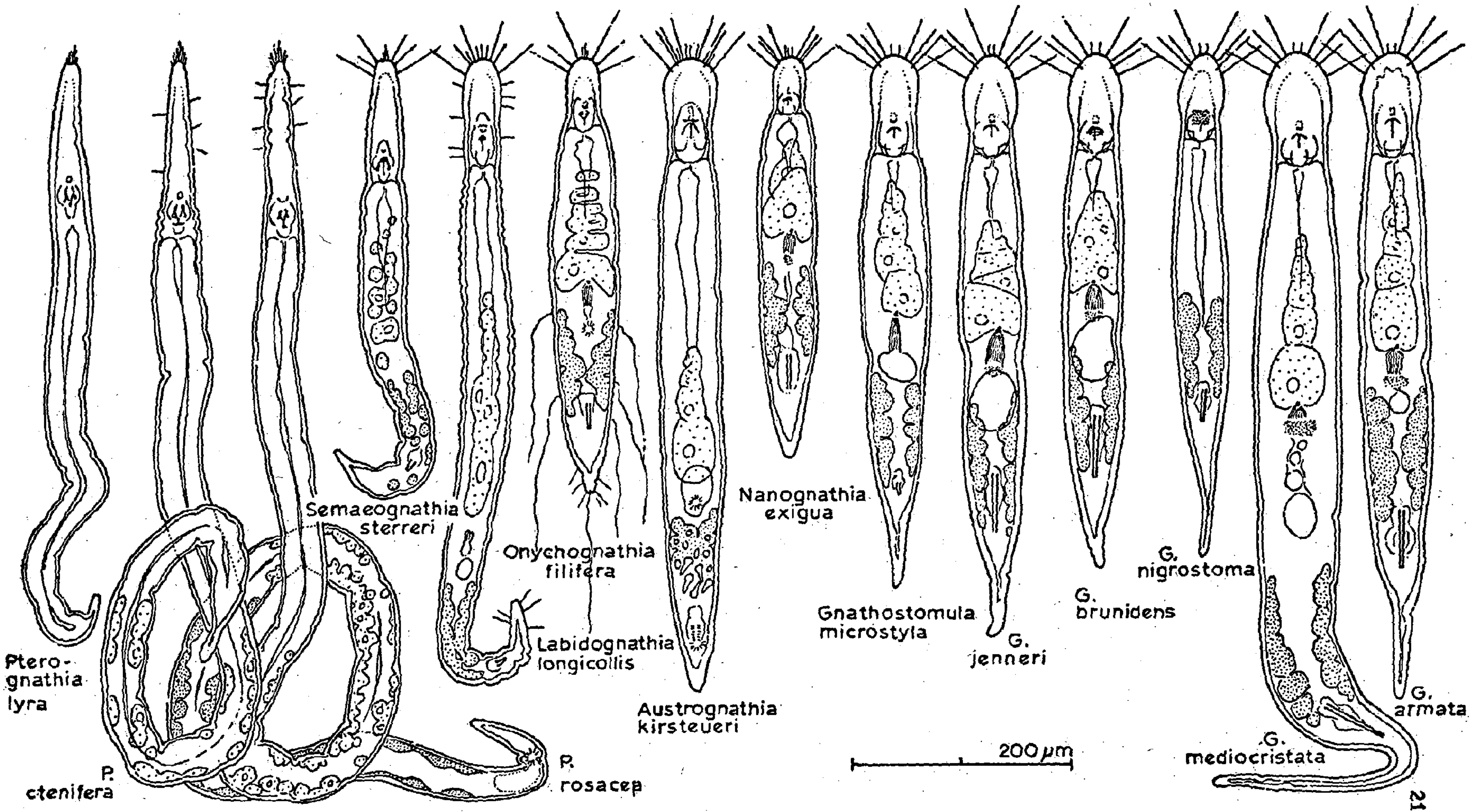

Ptero-
gnathia
lyra
P.
ctenifera
Semaeognathia
sterreri
P.
rosacea
Onychognathia
filifera
Labidognathia
longicollis
Austrognathia
kirsteueri
Nanognathia
exigua
Gnathostomula
microstyla
G.
jenneri
G.
brunidens
G.
nigrostoma
G.
mediocristata
G.
armata
200 µm

Fig. 31: Gnathostomulida, showing species known from the east coast of the United States (From Riedl 1969; Fig. 2).

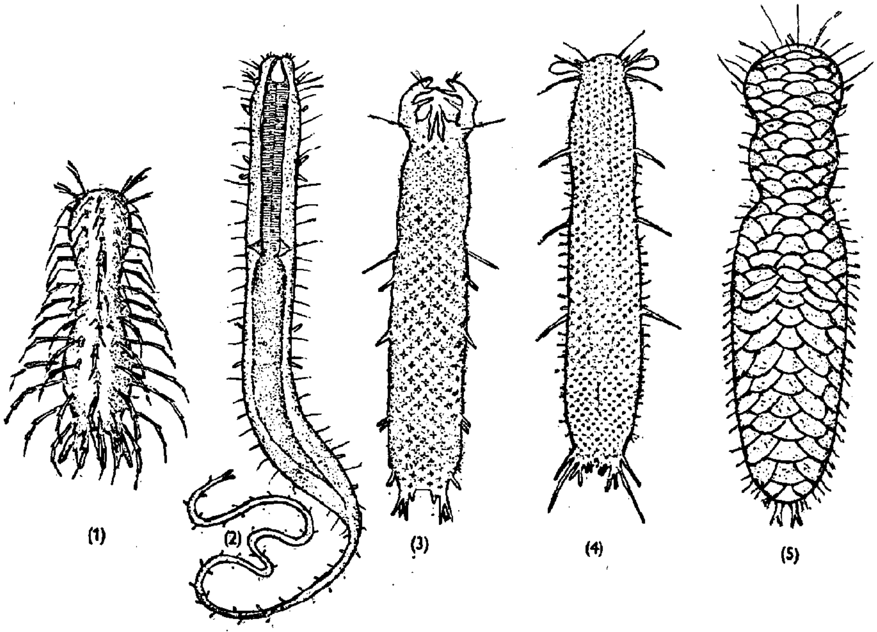


Fig. 32: Gastrotricha. (1) Order Chaetonotoidea, *Chaetonotus dispar* Wilke; (2-5) Order Macrodasyoidea; (2) *Urodasys viviparus* Wilke; (3) *Pseudostomella voscovita* Swedmark; (4) *Thaumastoderma heideri* Remane; (5) *Diplodasys ankeli* Wilke. Diagrams (2) and (5) modified after Wilke (From Swedmark 1964; Fig. 7).

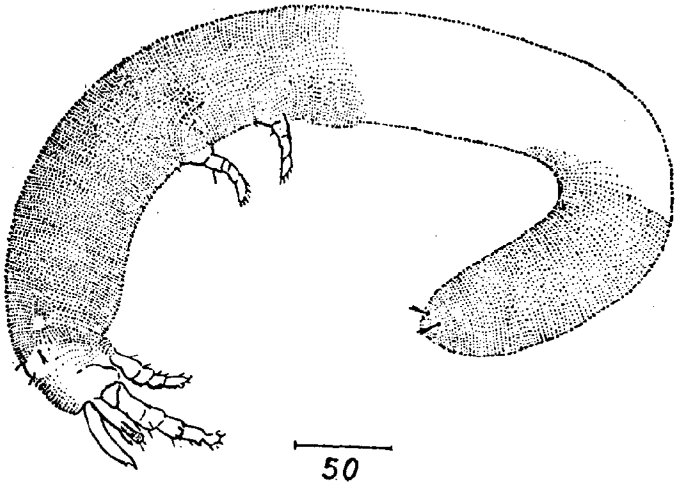


Fig. 33: *Nematalycus nematoides*, an interstitial mite (From Delamare 1960; Fig. 103).

largest fraction within the microfauna, as is true in nearly any environment (Wieser 1959).

Kinorhynchs (j), generally common in fine sediments, are represented in the interstitial environment by the new suborder Heterorhaga (Gerlach 1956). The Nemertini (k) are represented by the systematically isolated Ototyphlonemertini. Several unexpected types of archiannelids (l) are also typical of the mesopsammon and are nearly restricted to high energy beaches. Some of them are the smallest annelids known (350μ long). The large group of polychaetes (m) mostly consists of very small species of syllides and other families adapted to the pore system (Swedmark 1958). A remarkable number of Oligochaete species (n) are known from the interstitial, coastal environment, yet without special adaptations (Bulow 1957).

Crustacea (o) in the porous system are represented by six groups. First, Copepoda are present mainly in the form of harpacticids, often very slender types (Noodt 1952 and 1957). Second, Ostracoda also, but to a smaller extent, show elongation in their interstitial representatives. Third, Mystacocarida, a more recently discovered small group of conservative crustaceans, are strongly restricted to the sand environment (Delamare Deboutteville 1960). Fourth, among the Syncaridae, the Bathynellacea are found, particularly in tropical coasts. Fifth, Isopoda, which normally consist of larger species, in the sand Microparasellidae and Microcerberidae are very slender types, 0.8 to 1.5 mm long. Sixth, Amphipoda, very common in other bottom biotopes, show up in the interstitial space as microscopic Ingolfiellidea.

Tardigrada (p), mostly limnobiotic, in the marine environment are mostly restricted to interstitial life. Although among the smallest of metazoans they show most peculiar structure (See Fig. 4), particularly on tropical beaches (Renaud-Debyser 1963). Mites (q) are represented by relatively conservative marine groups such as Halacaridae as well as by very specialized types such as Nematalycidae (Fig. 33; Strenzke 1954). Small terrestrial anthropods (r) such as palpigrades or collembola are known (Monniot 1966, Delamare 1956) from the sand pore system.

Mollusca (s) have three main groups in the system. Solenogasters, known mostly from muddy bottoms have been discovered as very small species in the sand. The same is true for Placophora, until recently known only from stable substrate (Swedmark, Salvini-Plawen, unpublished). Gastropods are represented by strongly reduced groups such as the Rhodopidae, Pseudovermis and Microhedylidae.

Brachiopoda (t) were very recently discovered (Swedmark 1967) in the sand: a very small species of the new genus Gwynia (Fig. 34A). Bryozoa (u) are known to be present as the very curious solitary and migrating form Monobryozoon (Fig. 35A; Remane 1938). Echinodermata (v) are represented only by some holothurians, very small species such as Leptosynapta. Finally, Ascidiacea (w) are known, with an increasing number of species. All are nearly microscopical and solitary types with rhizoid threads deriving from different taxonomic groups of ascidians (Fig. 35 B,C. Monniot 1965).

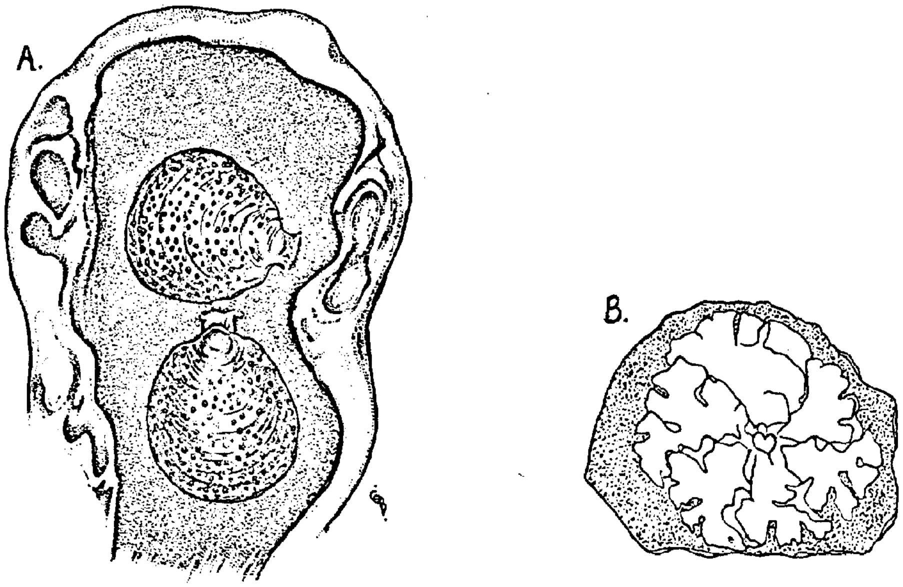


Fig. 34: Sedentary interstitial organisms. A. Two specimens of *Gwynia capsula* (Jeffreys), a brachiopod with brood protection, living within a serpulid shell fragment (From Swedmark 1967; Fig. 1). B. The foraminiferan *Discammina fallax* Lacroix attached to the surface of a sand grain (After Remane, from Delamare 1960; Fig. 61).

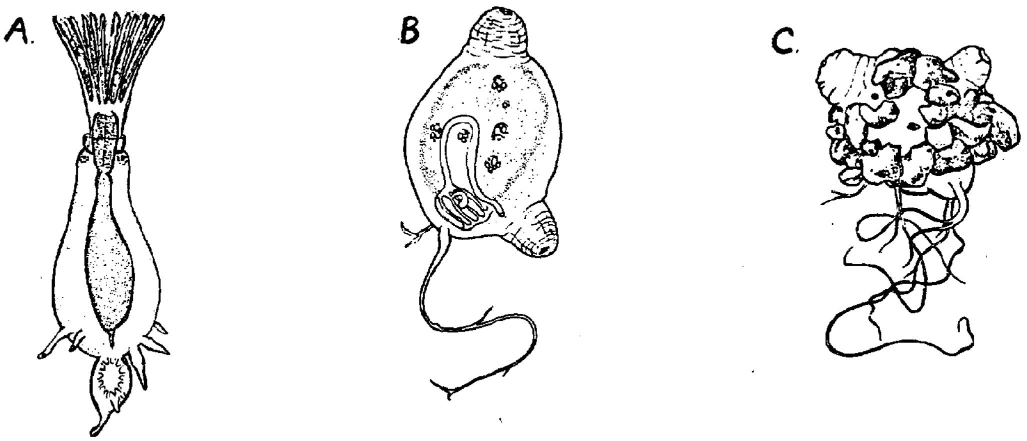


Fig. 35: Interstitial organisms. A. *Monobryozoon ambulans* Remane, an interstitial bryozoan (After Remane). B. and C. Interstitial ascidians, *Psammostyela delamarei* (Weinstein) and *Polycarpa pentarhiza* Monniot, respectively (After Weinstein and Monniot) (From Ax 1966; Fig. 11).

Adaptations and Species Selection

Structural adaptations

Structural adaptations, of course, or preselections at least, are indispensable for living in the interstitial environment.

Body size is the first unavoidable restriction. Groups with extremely small size such as gastrotrichs or tardigrades have no problems, and forms of extremely slender shape, such as nematodes, are practically preselected. Others, however, show most interesting reactions to this rigorous size test. It is not so astonishing that turbellarians adapt to such conditions. It is more so with regard to gastropods or higher crustaceans. But it is most unexpected to see such types as solitary ascidians or holothurians reduced to dwarf shapes that fit into the system.

One of the chances for larger animals to fit into the pore spaces is to take the "vermiforme" shape. This is particularly applicable to groups anatomically disposed to stretching (Figs. 3 and 4; Remane 1952). But groups without such an obvious predisposition such as isopods or amphipods, harpacticoids, gastropods or mites show to a **less** extreme extent the same ability. Clearly, other forms, such as the ostracods or brachiopods, do not join this channel of adaptation. In addition to the vermiform channel, the "leaf-shape" also gives new opportunities for interstitial dwelling for two types: (1) A few sedentary forms (for example, certain Foraminifera) have this shape which permits tight attachment to sand grains and hence protection against grinding and shifting sand. This shape also aids in keeping the necessary interstitial space open in the packed sediment. (2) Mesopsammon living in the moist zone, where the sand grains are covered with a thin water film, are also disposed toward such adaptation. These include mainly very small representatives of the mesozoa, the gastrotrichs (Chaetonotoidea) and tardigrades.

Formation of a tail in half a dozen of the groups composing the mesopsammon illustrates typical adaptive convergence (Fig. 4). The advantage of such a tail is related to that of adhesive organs and locomotion in the movable substratum. A contractile tail increases the locomotion-radius of an organism remarkably when it is still anchored by its caudal tip to a sand grain; quick retraction allows it to escape from a danger spot discovered with the anterior end, to a protective distance (Wilke 1954, Ax 1963). However, this organ may also be just a product of the process of diminution, as in ciliates or certain acoelous turbellarians which have adhesive organs. The first advantage, then, relates to locomotory stabilization, the final benefit may come in conjunction with the development of adhesive organs. This development of adhesive organs is an important contribution to life in high energy beaches. It is nearly indispensable for organisms living in the surface sand in the surf area. These organs are always present in gastrotrichs and gnathostomulids and in most turbellarians and tardigrades. In some turbellarians they have a striking similarity to ones known from gastrotrichs and have therefore become an often quoted example of convergence in the interstitial environment. Yet they are too small for proof of their possible structural identity to be obtained with the light microscope, and their ultrastructure is still unknown.

Locomotory adaptations

Besides size and general shape, locomotion becomes a restricting feature in a sand environment. Nearly without exception, interstitial creatures are vagile or at least have become semivagile through adaptation. Locomotion of the primarily vagile groups is more or less the same as in other environments: nonciliary gliding as in bluegreen algae; ciliary gliding as in ciliates, turbellarians, hydroids, gastropods (Fig. 36) and others; snakelike writhing as in nematodes and; crawling as in tardigrades and crustaceans. The adaptation of such primarily sedentary types as bryozoan and ascidian merits more attention. In both cases the semivagile types bear rootlike structures (See Fig. 35). In bryozoans these structures, used for anchoring and locomotion are reminicent of the common stolons connecting specimens within colonies. In ascidians they are used for anchoring (locomotion is due to body contractions) and are also normally common in solitary species. In these large original forms, however, they are tiny compared with the body size; in interstitial dwarf forms, on the contrary, they are often longer than the body length. Nonvagile forms within the sand biotope are chiefly algae, foraminifera and brachiopods. No details are known at present about small incrusting algae on sand grains. However, the incrusting foraminiferan and the sedentary brachiopod have been studied (Fig. 34). The sedentary life of the algae and foraminifera might be understood in terms of their rapid life cycles; the brachiopod appears in coarse material, and has a tendency to hide in the concave parts of shell particles (Swedmark 1967).

Sensory adaptations

Finally the sensory systems of the mesopsammon show specialization. Forms bearing eyes are very scarce (gastrotrichs), and in some interstitial groups such as Gnathostomulida or Otoplanidae they are lacking completely. On the other hand, statocysts, sensory cilia, or sensory bristles are very common, often very long or very regularly arranged (examples are otoplanides, gnathostomulides, and tardigrades.)

Reproductory adaptations

Reproductory adaptations are also known. The first involves sex cells and sperm transmission. The number of eggs produced by the mesopsammon is generally small, probably due to lack of space. The number may be drastically reduced to one ripe egg at a time (as in some gnathostomulids, isopods, and others). Also copulation predominates over simple release of sperms. Finally spermatophore production is more common than in other marine environments. Within the mesopsammon spermatophores are known in species of gastrotrichs, archiannelids, polychaetes, and gastropods (Acochlidiacea). These structures increase chances of fertilization, and avoid the loss of released gametes (probably a strong possibility in the three dimensional porous system).

Viviparity and brood protection, also remarkably developed in the mesopsammon, obviously lead to the same goal. Some groups such as isopods and amphipods already had brood protection before conquering the interstitial environment. Brood protection is also found in Otohydra (hydroid), in Nerilla and other archiannelids, and viviparity in Urodasys (gastrotrichs). But most

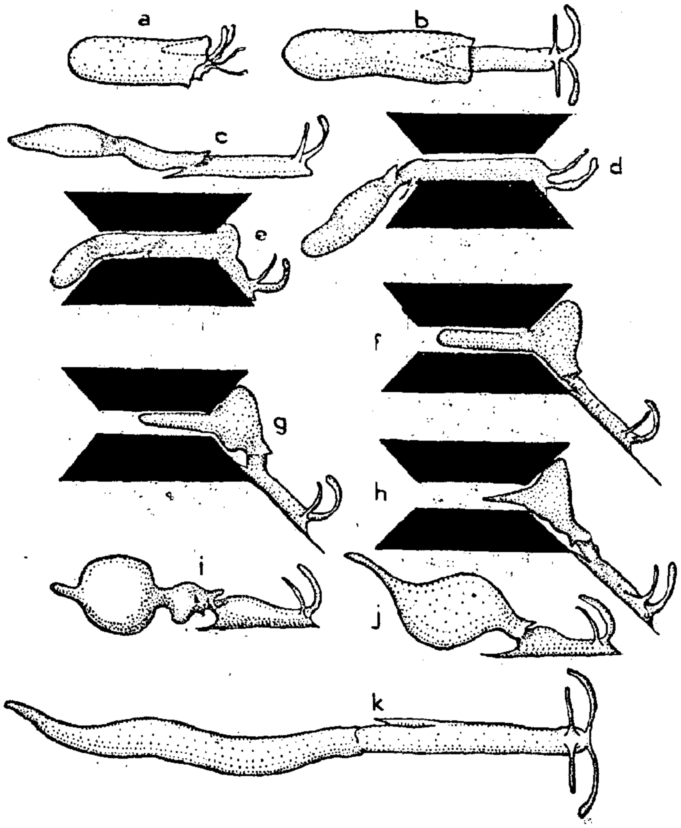


Fig. 36: Diagrammatic representation of locomotory progression of Unela odhneri (Delamare) between two grains of sand. a. b. c. k. Stages from contraction to full extension; d.e.f.g. progression between sand grains; i.j. peristalsis of visceral sac (From Delamare 1960; Fig. 55).

striking is the brood protection mechanisms of interstitial ascidians and in Gwynia (brachyopod) whose embryos, designed to become pelagic larvae, are kept until a more advanced stage of development (Swedmark 1967, Monniot 1965). The maintenance of species with low reproductive rates is made more certain with these adaptations. They also increase the chances of remaining in the biotope.

The tendencies toward benthic types of larvae, toward thigmotactic larval behavior and toward neoteny (maturity at an earlier stage of development)lead to similar ends (Fig. 37). In addition, neoteny also leads to diminution, which is important in this environment. The high percentage of groups without pelagic stages is remarkable: bluegreen algae, turbellarans, gastrotrichs, gnathostomulids, nematodes, tardigrades, isopods, amphipods and others. Only a small minority of species such as gastropods and archiannelides have free larvae. But they also tend to have the first part of their development protected within cocoons, and the hatched larvae are either reduced or they demonstrate no positive phototaxis and therefore no tendency to leave the substratum.

Behavioral adaptations

Gregariousness, or the tendency of specimens of a population to aggregate, has been observed in archiannelids (Boaden 1963, Gray 1966) and gnathostomulids (Riedl 1969). The function of gregariousness is to keep groups of the population in closer contact, a tendency which, particularly within the porous system and in less dominant species, might be of biological importance. Thigmotaxis and positive geotaxis, the tendencies to stay in contact with the substratum and to orient toward the direction of gravity, are generally common in all interstitial groups. Some groups (Acoela and Gnathostomulida), if kept in a petri dish without sand, move ceaselessly for hours, seemingly searching for a hollow leading downward until they finally die. The mortality rate is also much higher in many interstitial groups if they are kept without substratum (Riedl, unpublished), a phenomenon which merits detailed study.

Physiological adaptations

Physiological restriction to areas of high oxygen tension is obvious in some groups of turbellarians (Otoplanidae) and gastrotrichs. However, the observations are based only on emigration behavior and mortality rates during deterioration of the microclimate. Some information on adaptation to lack of oxygen in gnathostomulids (Riedl 1969), some turbellarians (Catenulida), and bluegreen algae can be derived from observing their zonation in the sediments. Closer investigations, however, are desirable.

Trophic Relationships

The trophic situation within the mesopsammon subsystem is characterized by low primary productivity, a small number of filterers, a large number of highly diverse so-called detritus feeders, a limited selection of diatom-feeders and predator types, and an important contribution of decomposers.

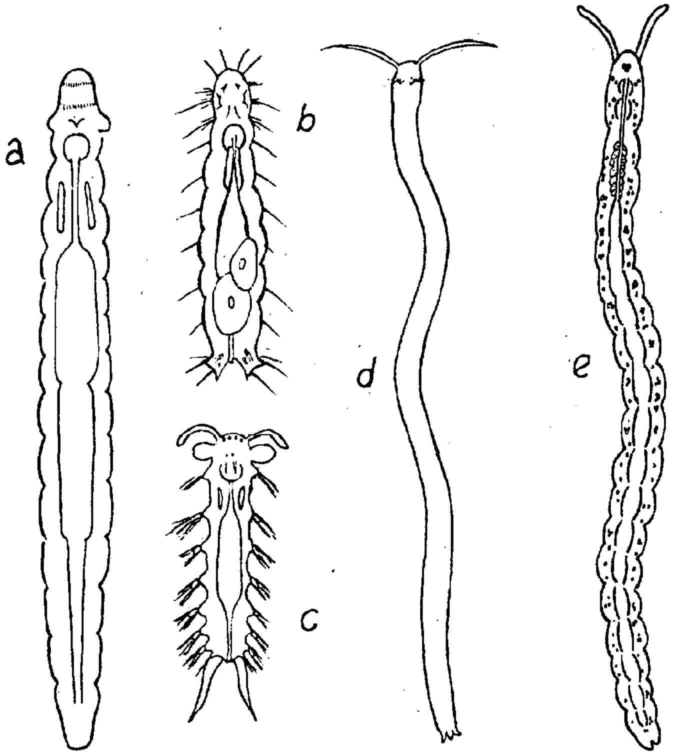


Fig. 37: Neotenic forms of archiannelid adults.
a. Trilobodrilus heideri Remane; b. Diurodrilus minimus; c. Nerillidium gracile; d.e. Protodrilus (After Remanes from Delamare 1960; Fig. 50).

Autotrophs

Autotrophic or primary production is restricted to the first millimeters of sand surface and is due mainly to the activity of some bluegreen algae and diatoms. They can be brought to deeper layers, through the movement of the substratum, but cut off from sun energy, there is no assimilation in these layers. Therefore mixing of the top layers with deeper strata does not increase productivity but only food distribution. Recently other strata of (mainly) bluegreen algae have been found within the deeper, oxygen deficient, "black layer" (Riedl, unpublished). As yet, the contribution of these saprophytic groups to the system has not been studied.

Filter feeders

Filter feeders which channel suspended food directly to the system are strongly restricted in the interstitial environment. Only Monobryozoon (bryozoan) and Gwynia (brachiopod), rare species, clearly belong to this group. This is strange because of the high wave energy, providing for transportation of suspended matter. However, the strong reduction in current within the porous structure, as well as the very restricted space conditions there might not allow a greater contribution of this very successful ecological group.

Detritus feeders

So called "detritus feeders" are, by far, the most common group. The species of all key groups of the mesopsammon, with the exception, perhaps, of the nematodes belong to it. This huge ecological group has been divided (By Remane 1933a) into four subtypes, based on mechanics of food uptake: Browsers (gnathostomulides, archiannelids, harpacticoids, ostracods, molluscs), pumpsuckers (turbellarians, gastrotrichs, many nematodes, some polychaetes), puncture-suckers (tardigrades), and sand-lickers (cumaceans, certain amphipods) mostly belonging to the endofauna.

Without any doubt, detritus feeders form the strongest and in a sense the primary link in the food chain of the mesofaunal subsystem. Therefore a strong inflow of "detritus" forming the basic energy sources for a majority of interstitial life can be assumed.

However, "detritus" and "detritus feeders" are vague conceptions and often (due to an almost complete lack of knowledge concerning the biology of most of the species) a group is labelled as detritus feeding only because of absence of formed food particles in the gut as observed with light microscopy. They may be feeding on small bacterians, sucking on bluegreen algae, or collecting dissolved organic matter. This problem becomes particularly challenging since the key groups which are nearly restricted to mesopsammon, gnathostomulids, gastrotrichs, marine catenulids (Sterrer, Riedl, unpublished) and tardigrades belong almost entirely to this ecological feeding type.

Diatom feeders

Diatom feeders, a small percentage, are nearly randomly distributed within these key groups. Some species of Acoela (turbellarians), harpacticids and other taxa show diatoms quite regularly in the gut; others are too small to swallow whole diatoms. However, the number of specialized diatom feeders may have been over-estimated, because often diatoms may be ingested by chance.

Predators

Predators are represented but strongly restricted to the very small interstitial types. The interstitial ceolenterates in particular belong to this group. The same is true with regard to two turbellarian groups (otoplanids and kalyptorhynchians). The former, however, are normally scarce, the latter are generally restricted to surface layers, and both are correlated with coarser sands. The most abundant predator group is probably the nematodes. According to their pharyngeal organization (Wieser 1953) many endopsammon nematodes seem to belong to this group.

Decomposers

Decomposers within the interstitial system are of great importance. Humm (in Pearse, Humm and Wharton 1942) has shown an average of 200,000 bacteria per gram of sand in the interstitial zone at Beaufort, N.C. The highest count was 1,250,000, the lowest 5,000/g. An increase from low tide through mid-tide to high-tide level was found; the average values ranged from 34,000 over 110,000 to 486,000 per gram of sediment. In general, the number of bacteria increases as the particle size decreases (ZoBell 1938) or when the percentage of organic matter rises.

The distribution and activity of bacteria also varies within the different sediment strata. This is demonstrated by the formation of ferrous sulfide (Bruce 1928b) in the deeper black layer. The important contribution of bacteria to the beach system merits much closer examination.

Patterns and Causes of Species Distribution

Among the important parameters limiting the distribution of organisms in high energy beach systems under natural conditions are desiccation, salinity, fine sediments and coarse sediments. Desiccation, of course, is one of the chief dangers for marine life in the sand environment, but rising seas, high capillarity and spray water help alleviate it. Furthermore, the smallest inhabitants of the interstitial space (for example, Tardigrada) are often only 0.3 mm long and less than 0.05 mm high. This dwarf size enables several species to live within the fine water film surrounding sand grains that are only moist.

Freshwater boundaries and rigorous salinity changes caused by tide movement are also limiting. At the ground water level conditions are much more buffered and a wide brackish zone with a special fauna, mostly marine migrants, connects the marine and the subterranean freshwater biotope.

Fine sediment limits the occurrence of the interstitial fauna in two different ways. First, a reduction in the main grain-size-fraction down to 200 or 150μ excludes progressively all types of the mesopsammon. Second, the addition of fine sediment to a sand body soon chokes the interstitial system.

In cases of tight packing and in less sorted sands (having a broader variety of grain sizes) the amount of fine sediments required to close the interstitial space can be very small.

Too coarse sediment gives rise to a marine desert. There is a size category (cobble) between coarse sand and boulders that is too large to provide the conditions of the interstitial environment, but too small to offer a stable substratum for sedentary groups. Such "sediments" often lie as a limited layer on flat rocky planes at or underneath low tide level. During stronger surf action the whole layer moves, forming a deadly mill and grinding all living structure between them. On days with quiet seas, smoothly polished rock banks with traces of scrubbing mark the boundaries of this layer, which adjoins the higher exposed areas at the surf level on younger rocky shores. Fine sediment regions, on the other hand, are more common in sheltered areas and are always found at greater depths.

All biological patterns are in a permanent process of transformation. In order to gain a position from which to describe the processes involved in the patterning of species distribution in beach systems, we are forced to assume and to describe first a relatively stable situation. Furthermore, the causes of species arrangement, the degrees of correlations between them, the amount of information available, and the degree of our understanding varies strongly from case to case. Primary and secondary causes of species distribution will be discussed separately; correlation and an attempt at understanding will follow.

Primary patterns

Primary patterns are those caused by environmental factors directly and not indirectly, as by species interactions. Such primary factors are mainly the inorganic gradients, but include also the energy gradients, including food import. Today almost all our information regarding causes of biological patterns within the high energy beach system is related to environmental factors. This is due to a certain extent to the great hydrodynamic stress from the ocean, leading to an unusual predominance of influence of the physical parameters and to high specialization of the edaphic conditions. In other systems, such as coral reefs, mangrove swamps, sea caves, and algae beds, secondary patterns are known to regulate many subsystems, but even in these systems, primary patterns were the first to be understood. Therefore, the situation with regard to sand systems may be due to the preliminary stage of our knowledge.

Species patterns may be analyzed by the descriptive approach of studying zonation first in its broadest sense; analysis then leads to component correlations and synthesis to an understanding of the subunits or associations within the system.

Zonations may be considered as the result of a combination of gradients. They are three dimensional and vary in their scales from micro- to geographic distributions.

Beach profiles have been divided into from three to five zones, according to the species (Davenport 1903, Schultz 1937, Dahl 1953) and the local geomorphology. The backshore area, or subterrestrial fringe, can be characterized by talitrid amphipods, by the ghost crab and by the lack of marine mesofauna in the drying surface sand. The frontshore region can be divided into three biological zones according to local conditions: the moist area or the slope contains corophiids on the surface and tardigrades and mystacocarids below the surface. The low water terrace contains typically burrowing arenicolids, thalassinids, cirolanids (isopods) and gnathostomulids in the black zone underneath. In the surf zone Emerita and Donax of the endofauna, and otoplanids of the mesofauna are most characteristic. In the offshore zone diversity again increases, including very distinct microzonations of nematodes, harpacticoids, turbellarians, and even shrimps (Ax 1951, Gerlach 1948, Noodt 1957 and others; Fig. 38). However, our knowledge cannot be generalized yet on a worldwide scale.

Vertical faunal layering is clearly developed, but it varies strongly from zone to zone. In the backshore, for example, there are mainly three layers related to humidity, salinity and temperature changes. Terrestrial dwarf arthropods populate the dry top layer, tardigrades and mystacocarids are mainly in the underlying moist layer and archiannelids, malacarids, isopods and amphipods are in the groundwater layer. In the offshore zone, on the other hand, the surface layer holds filter feeders while the deeper strata are layered according to oxygen availability, with only nematodes in the lowest populated part.

Coastal sequences, the faunal changes along the coast, are mainly related to exposure, sand grain size and coastal angle as is clearly shown in the meso- and endofauna. Mollusc zonation ranges from Olivia and Donax types in exposed areas to Nassarius and Tagelus in sheltered, muddy, fine sand flats (Fig. 2). Many examples can be given within mesofaunal groups.

Much less is known of species zonation within the larger scale of geographic sequences. However, within the macrofauna (Figs. 39 and 40, Dahl 1952, 1953) and particularly in cases where more information is available, as in lugworms (Fig. 41) geographic patterns become very clear.

Correlations of factors determining zonation are usually made using field ecological approaches at first, and are later studied under laboratory conditions. Climatic, edaphic and xenotrophic factors (i.e. food sources from outside the system) are involved (Jansson 1968).

Humidity deficiencies reduce the fauna to smaller size classes and to life in thin water films covering the sand grains. Presumably, a change from marine to terrestrial types of interstitial fauna occurs when the air spaces increase between sand grains.

Light influences first of all the distribution of autotrophic plants, mainly diatoms, within the surface layers. But archiannelids also because of their light sensitivity are kept within a well-defined layer (Gray 1966).

Temperature affects many species in the foreshore and particularly in the backshore regions leading to avoidance of areas of higher temperature or high temperature change, or to migration into deeper areas during hours of most intense radiation. Temperature stability within the groundwater, on the other

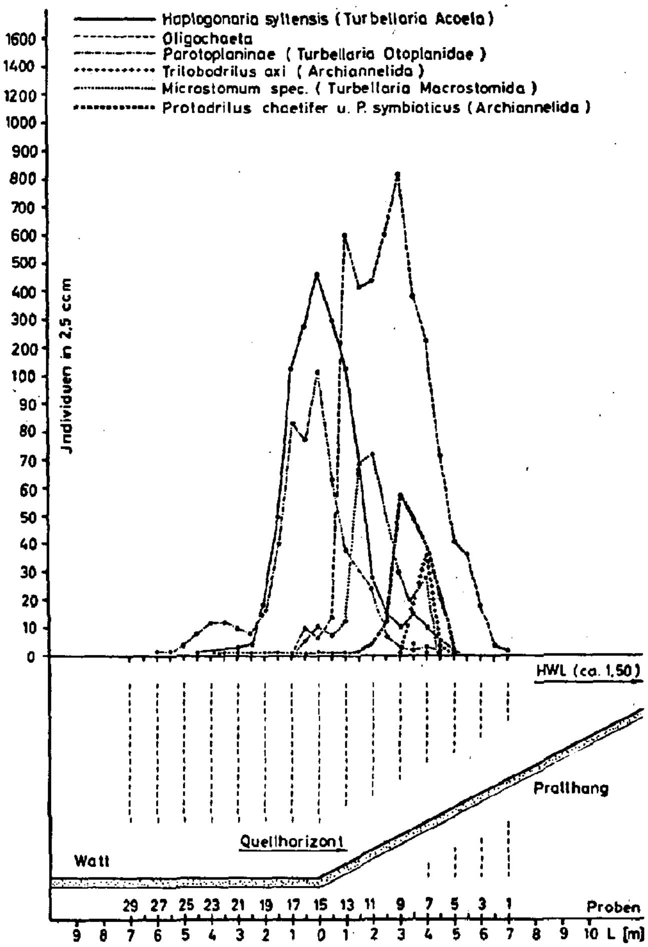


Fig. 38: Microzonation within the well horizon (quell horizon) of the North Sea in July 1964 showing distribution of 6 species of the mesopsammon (From Doerjes 1968; Fig. 10).

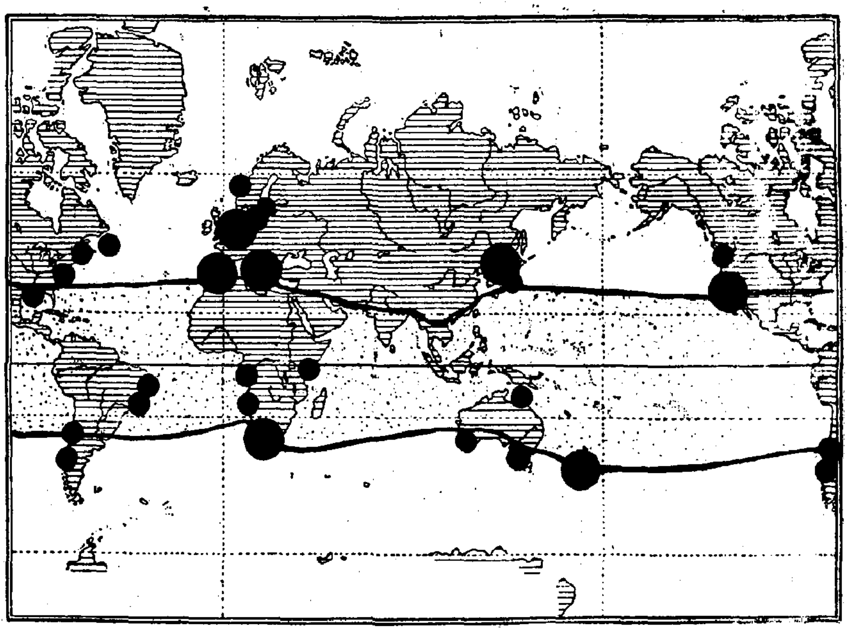


Fig. 39: Distribution of talitrid amphipods which dig in sandy beaches, and of the crab genus Ocypode. Black circles indicate location and number of amphipod species (1-4) with this ecology. Distribution of Ocypode is shown by the stippled area between black lines (From Dahl 1952; Fig. 6).

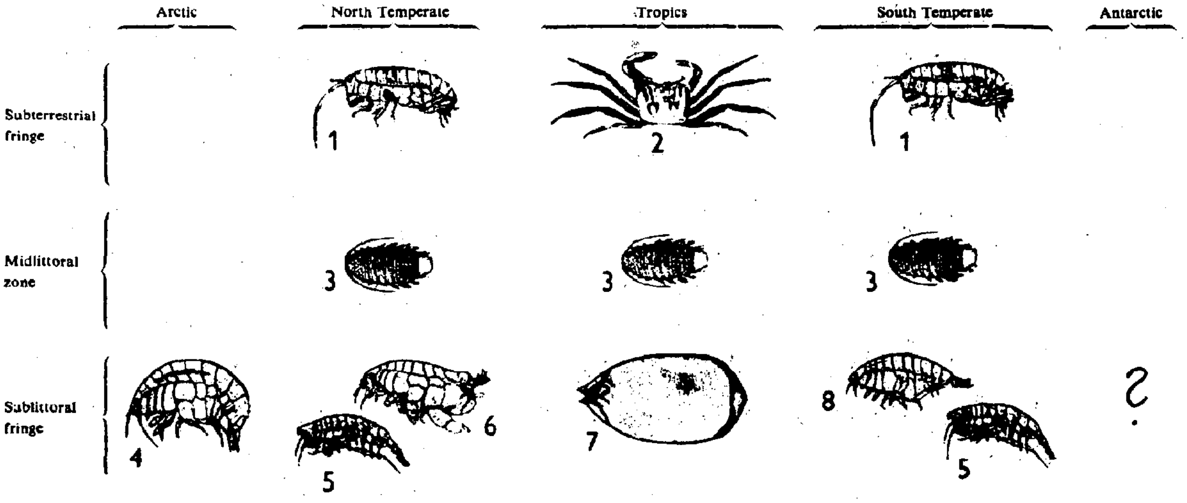
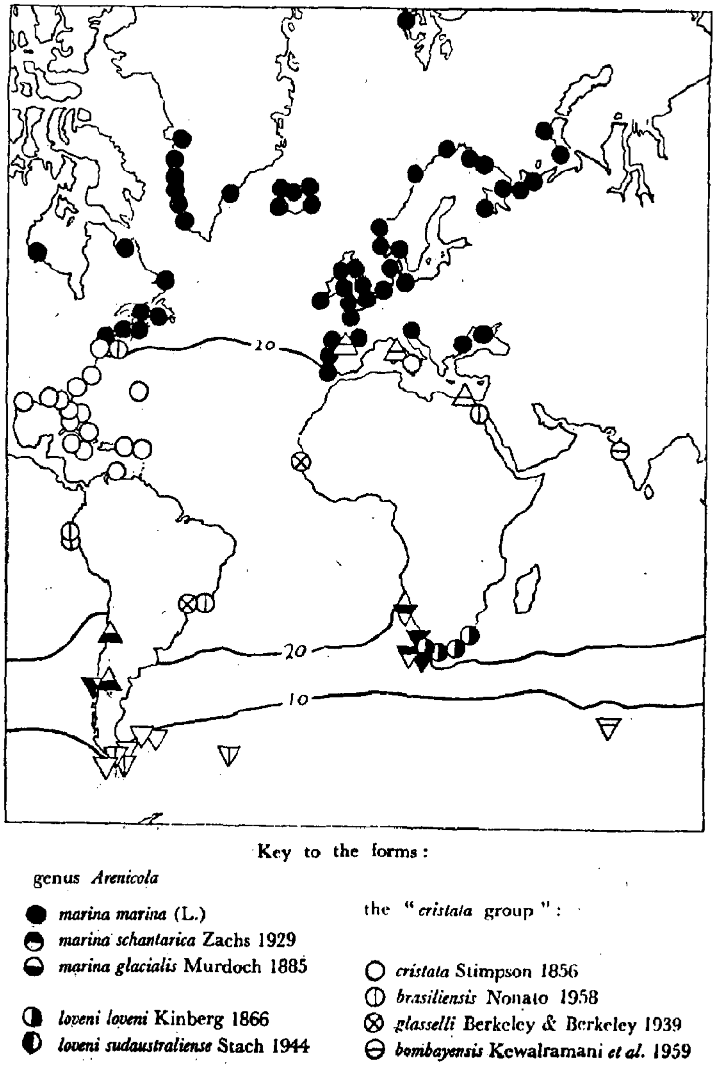
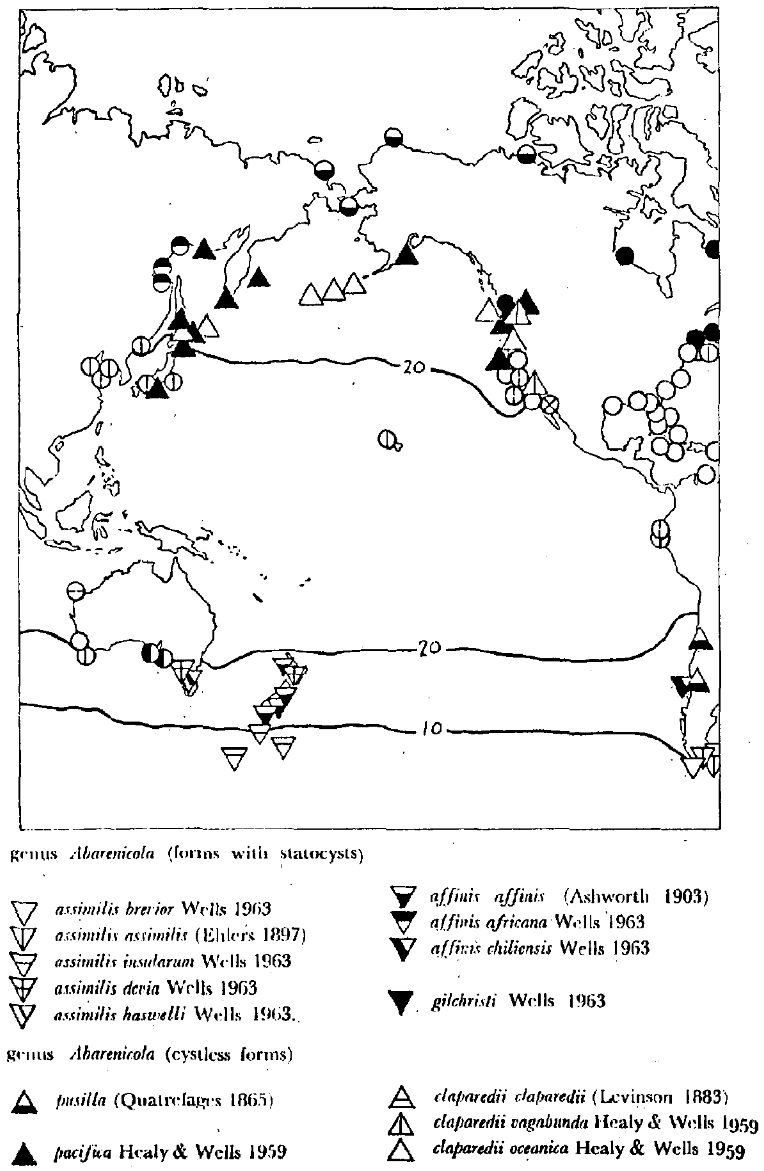

Arctic
North Temperate
Tropics
South Temperate
Antarctic
Subterrestrial fringe
Midlittoral zone
Sublittoral fringe
1
2
1
3
3
3
4
6
5
7
8
5
?

Fig. 40: Generalized diagram showing zonation of sandy beach crustaceans in the main climatic zones of the earth. 1. Talitrid amphipods; 2. ocypolid crabs; 3. cirolanid isopods; 4. lysianassid amphipods (genus Pseudalibrotus); 5. oedocerotid amphipods; 6. haustoriid amphipods; 7. hippid crabs; 8. phoxocephalid amphipods (From Dahl 1952; Fig. 8).



20
20
10
Key to the forms:
genus *Arenicola*
● *marina marina* (L.)
◒ *marina schantarica* Zachs 1929
◓ *marina glacialis* Murdoch 1885
◑ *loveni loveni* Kinberg 1866
◐ *loveni sudaustraliense* Stach 1944
the "*cristata* group":
○ *cristata* Stimpson 1856
⦶ *brasiliensis* Nonato 1958
⊗ *glasselli* Berkeley & Berkeley 1939
⊖ *bombayensis* Kewalramani *et al.* 1959

Fig. 41A: World distribution of the lugworm genus Arenicola (From Wells 1963; Fig. 5).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genus Abarenicola (forms with statocysts)
assimilis brevior Wells 1963
assimilis assimilis (Ehlers 1897)
assimilis insularum Wells 1963
assimilis devia Wells 1963
assimilis haswelli Wells 1963.
affinis affinis (Ashworth 1903)
affinis africana Wells 1963
affinis chiliensis Wells 1963
gilchristi Wells 1963
genus Abarenicola (cystless forms)
pusilla (Quatrefages 1865)
pacifica Healy & Wells 1959
claparedii claparedii (Levinson 1883)
claparedii vagabunda Healy & Wells 1959
claparedii oceanica Healy & Wells 1959

Fig. 41B: World distribution of the lugworm genus Abarenicola (forms with statocysts) (From Wells 1963: Fig. 5).

hand, is one of the main factors permitting the existance of its typical fauna.

Salinity gradients affect faunal distribution in three dimensions. First, there is a remarkable faunal change from the purely marine, through the brackish, to the limnic groundwater zones. The same is true for salinity changes in the surface sands, from open marine shores to freshwaters in estuaries (Fig. 42). The third faunal change occurs between groundwater and surface sands in the upper foreshore region.

With changes in respiratory gas levels, dramatic changes in the fauna are to be observed. With increasing depth into the sediment, oxygen vanishes and turbellarians start to disappear (as shown by Jansson 1967). Numbers of nematodes also decrease. At the same time, saprophytic bluegreen algae, gnathostomulids and a new suborder of catenulid turbellarians increase (Riedl, unpublished).

Earlier it was assumed (Wilson 1952, Pennak 1951, Delamare 1953) that purely calcarous sands would bear no interstitial fauna, or at least a very restricted one. This, of course, has been disproved (Renaud 1955). The fauna of this almost always tropical organogenic sand may be as rich as that within quartz sands. However, our information is still in a preliminary stage.

Sand grain size is clearly a dominant factor in the distribution of many groups studied. It determines the lower limits of porous space available for interstitial fauna. Among the endofauna are species such as cumaceans (Wieser 1956) which show a very distinct preference for grain sizes less than 160μ which they are able to turn easily in order to lick the epigrowth. Distribution of mesofaunal species depends on space dimensions, as shown with hydroids, turbellarians, gnathostomulids, gastrotrichs, archiannelids and others (Boaden 1962, Gray 1967, Riedl 1969, Schrom 1966, Swedmark 1957, Sterrer 1965, Wieser 1959). The lower grain size limit has been drawn at around 200μ (Fig. 43) for most groups, but gnathostomulids can exist in sand with grain size at 150μ and less (Wieser 1959, Jansson 1967, Riedl 1969).

Food input, mainly from the sea, also affects faunal distribution. Population density increases near surface strata and in proximity to wave activity. However, the relation between pelagic food sources, hydrodynamic forces, and grain size and the filtering function of the sand is still unknown.

Subunits of faunal grouping within the high energy beaches can be proved statistically and described as associations of species which are regularly to be observed. The causes of such associations and their function will be discussed, but our knowledge is limited and no overall picture can be drawn on a worldwide scale. Six examples will be given.

1. A low-water-step or well-horizon fauna (Fig. 38) has been defined (Remane 1933a). It is characterized by the dominance of otoplanids (turbellarians) and seems to have a worldwide distribution. The subsystem is characterized by high energy input, groundwater outflow, coarse and strongly moving sediments and exceedingly quick and haptic species, mainly predators. It may have a certain autonomy in that beached plankton and stranded meiofauna are the main food

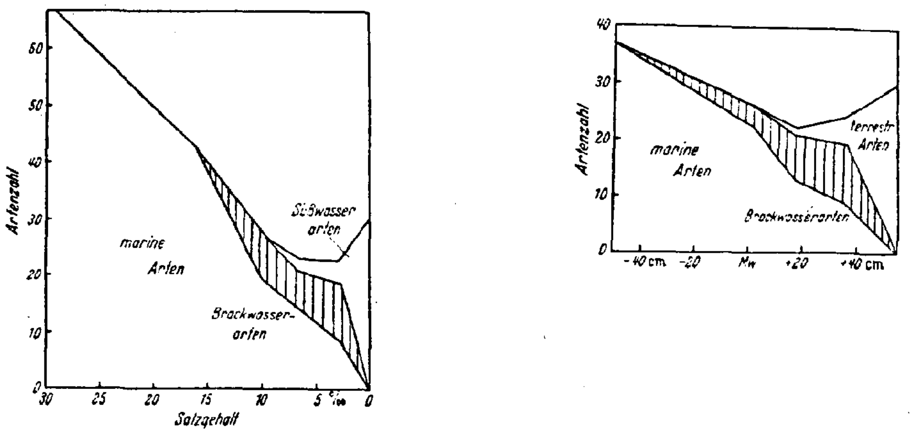


Fig. 42: Nematode zonation within the shore slope. Species number in relation to salinity (A) and to sea level (B). Marine species are represented at the left in each figure, freshwater or terrestrial species at the right, and brackish water species are between (lined area) (From Gerlach 1953; Figs. 10, 11).

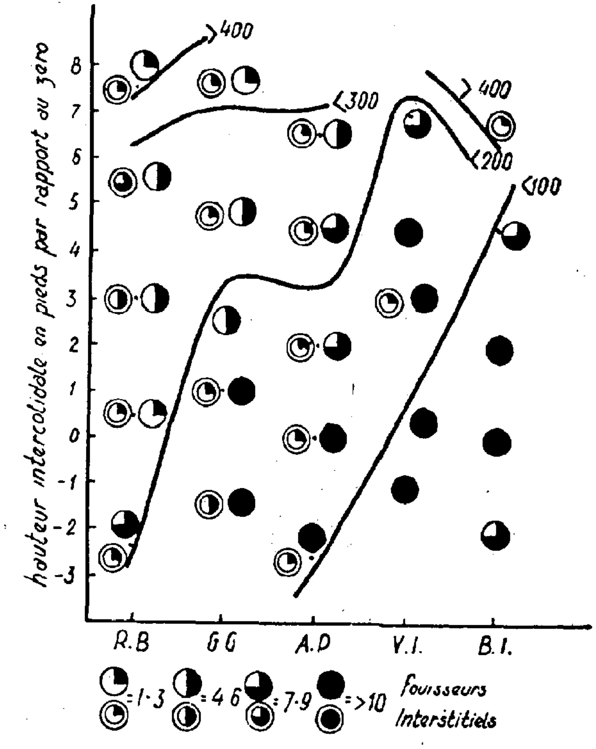


Fig. 43: Distribution of endo- and mesofauna in relation to grain size in five locations along Puget Sound. "Fouisseurs" refers to digging organisms (endofauna) and "interstitiels" to interstitials (mesofauna) (After Wieser 1959, from Delamare 1960; Fig. 27).

sources.

2. A passive migratory layer covering the whole foreshore area has similarities to the low water step fauna (Rieger and Ott 1969). A selected group of very long and slender acoels, kalyptorhynchs and coelogynoporids (turbellarians), and nematodes migrate with the shell material up and down with the tide. Using the surface material as a lift, they benefit by remaining constantly within the zone of maximal energy input.

3. The humid zone, an area "between interstitial tide-marks" including the space of capillary forces above it, is characterized by infiltration of air within the interstitial system. Capillary forces bring fresh and brackish water to the surface, evaporation takes place and salinity increases. Rainfall and heavy surf influence this balanced situation. The fauna has strong brackish water elements (Gerlach 1963) but also terrestrial components. A certain autonomy from the other interstitial environments is based on its food sources. Wrack material (higher algae and seaweed) often becomes imbedded in and important within the humid zone, forming layers of detritus in various stages of decomposition.

4. The brackish ground water bed underneath the backshore area is characterized by various archiannelids, copepods, isopods and amphipods in all stages of adaptation to subterranean freshwater. Very small (0.5 to 2.0 mm) and slender types are selected (Fig. 44). The independence of this subsystem is based mainly on its food source, detritus brought in by the current of continental groundwater.

5. The black zone in the deeper fore- and offshore area, bounded by a strong redox-discontinuity layer (Bruce 1928b, Pennak 1951, Perkins 1957, Fenchel 1969), can also be defined by its lack of oxygen, by its special fauna of (mainly) gnathostomulids and catenulids (Riedl 1969), and by its unusual food sources, including anaerobic bacteria and saprophytic bluegreen algae (Riedl, unpublished).

6. Finally, a whole series of zones between the exposed and sheltered extremes of the sand beach have been defined, mainly in terms of dominant species of the sand surface (Remane 1940, Ax 1951, Gerlach 1953, Noodt 1957, Bilio 1963), very characteristic for the Baltic Sea (Fig. 45).

Secondary patterns

Secondary patterns of species distribution are found within the endo- and mesofauna. Species arrangement in these cases depends on groupings based on primary distribution patterns. Since clarification of most interspecies relationships is still lacking, much less information is available on secondary patterning.

Within the endofauna, a surprisingly great amount of commensalism has been discovered. Some groups (e.g. erycinacean bivalves) show a high percentage of commensal types, and "most of the hosts are slow moving, almost sessile forms, which burrow in sandy or muddy bottoms" (Boss 1965). In a more primitive stage the commensal is not very selective; sedentary animals such as entoprocts and

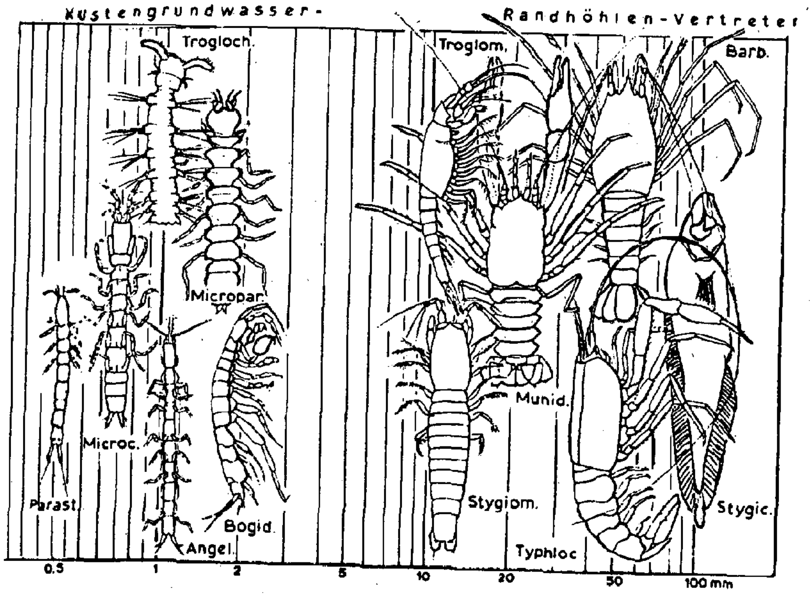

Küstengrundwasser-
Randhöhlen-Vertreter
Trogloch.
Troglom.
Barb.
Micropar.
Microc.
Parast.
Bogid.
Angel.
Munid.
Stygiom.
Typhloc.
Stygic.
0.5
1
2
5
10
20
50
100 mm

Fig. 44: Relationship of body size of organisms to the chosen immigration route from the sea to subterranean freshwater. Left, interstitial migrants; Right, sea cave migrants (From Riedl 1966, Fig. 142).

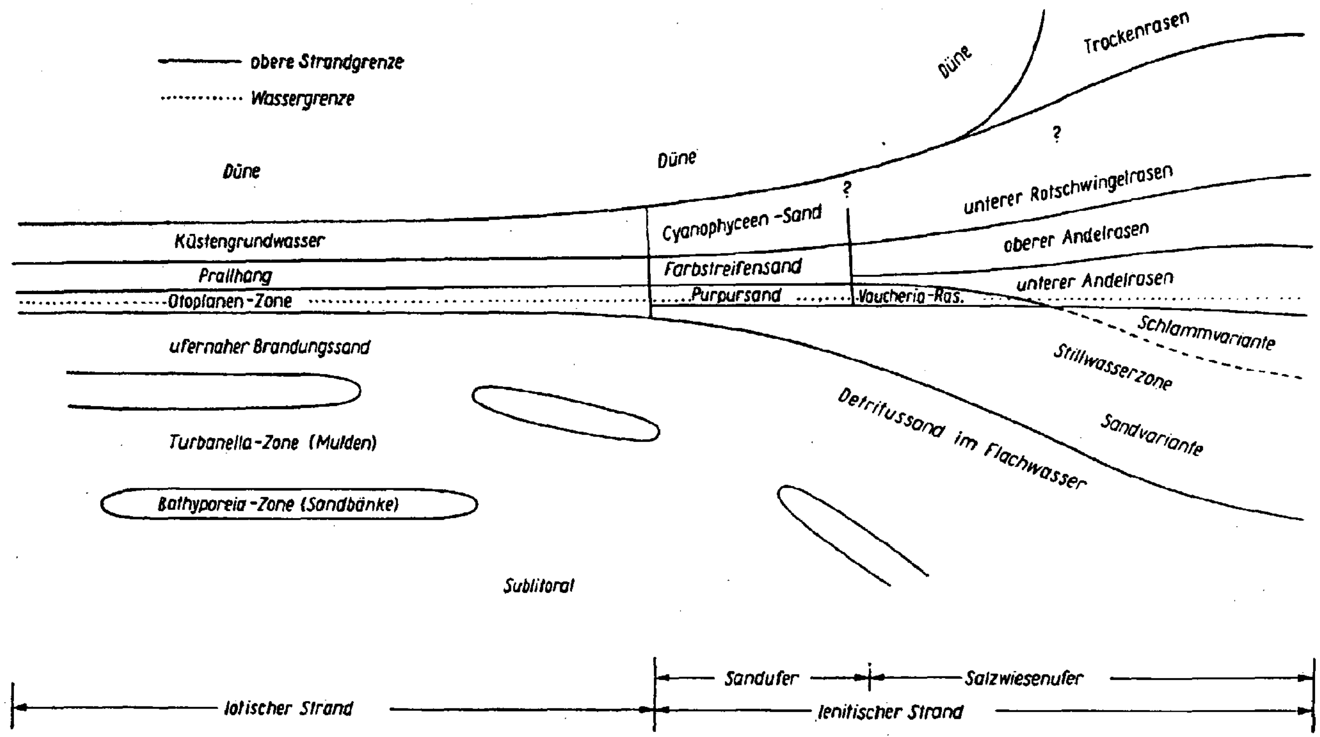

obere Strandgrenze
Wassergrenze
Düne
Düne
Düne
Trockenrasen
?
?
unterer Rotschwingelrasen
oberer Andelrasen
unterer Andelrasen
Küstengrundwasser
Cyanophyceen-Sand
Prallhang
Farbstreifensand
Otoplanen-Zone
Purpursand
Vaucheria-Ras.
Schlammvariante
Stillwasserzone
ufernaher Brandungssand
Sandvariante
Turbanella-Zone (Mulden)
Detritussand im Flachwasser
Bathyporeia-Zone (Sandbänke)
Sublitoral
Sandufer
Salzwiesenufer
lotischer Strand
lenitischer Strand

Fig. 45: Chart showing patterns of the main coastal environments in relation to distance from the water's edge. Ordinate is distance from water's edge (represented by dotted line. Abscissa give exposure index, from strongly exposed (left) to very sheltered (right) (From Bilio 1963; Fig. 3).

hydroid species use the shells of living clams (Donax) and crabs (Emerita) as a relatively stable substratum. The strong hydrodynamic action offers excellent conditions for them, and the migrating macrofauna, which travel with the tides and settle in the surface layer, offer adequately stable surfaces for attachment.

However, the macro-species are even more attractive to commensals if they provide true stability. This is particularly the case for types settled in relatively permanent tubes such as arenicolids (lugworms) and thalassinids. Up to nine different commensals are known to populate a single species (Fig. 46). Although this seems to be a high amount of commensalism, more recent papers have made it clear that discovery of new commensal relationships will continue (Sanders et al., 1962, Jenner and McCrary 1967). Obviously living stability (i.e. stability provided by macrofauna which adapt and compensate) creates oases of high attractiveness within an environment of great food supply but of unfavorable changeability.

For the meiofauna of the endopsammon, information is too limited to permit drawing a more general picture. We do not know whether this lack is based more on greater difficulties in observing species correlation in the psammon or more on a true reduction in inter-species relationships, due perhaps to edaphic limitations or difficulties.

Within the microscopic mesofauna true commensalism is also detected. It mainly involves syncarids and interstitial isopods and amphipods bearing commensal suctorians (Delamare 1960; Fig. 47). The majority of interspecific relations, however, such as that of predator and prey are not yet clear. This is because they have no permanent and solid contact, and because direct observation is not possible. All information must come first from statistically significant correlations; causes and effects will have to be analysed afterward. It can be predicted for example, that the distribution of diatom feeders will be correlated with algae zonation and so on; however, we do not know how selective most of the grazers and predators are.

A few examples may illustrate the complexity to be expected. Colonization experiments with sterilized sand within the natural environment have demonstrated that diatoms, diatom-feeders, and predators follow each other in sequence (Boaden 1962, Renaud-Debyser 1963). The zonation of some gnathostomulids within the black layer is almost identical with that of one of the bluegreen algae in this area; a direct connection therefore is probable (Riedl, unpublished). Finally, choice experiments have shown that Turbanella (gastrotrich) avoids a sediment which is or has been populated by Protodriloides (archiannelid).

The degree of interspecific correlation is important mainly in elucidating the structure of a biotope, but in the sand environment it is less clear than in other near shore biotas. This may be due to the tender age of psammology as well as the peculiarities of this three dimensional, opaque, and shifting substratum.

Actually, modern psammology is still in the descriptive stage, since not even all the main types of its biota are yet described, and large geographic areas remain completely unexamined. In some areas, as in the north European

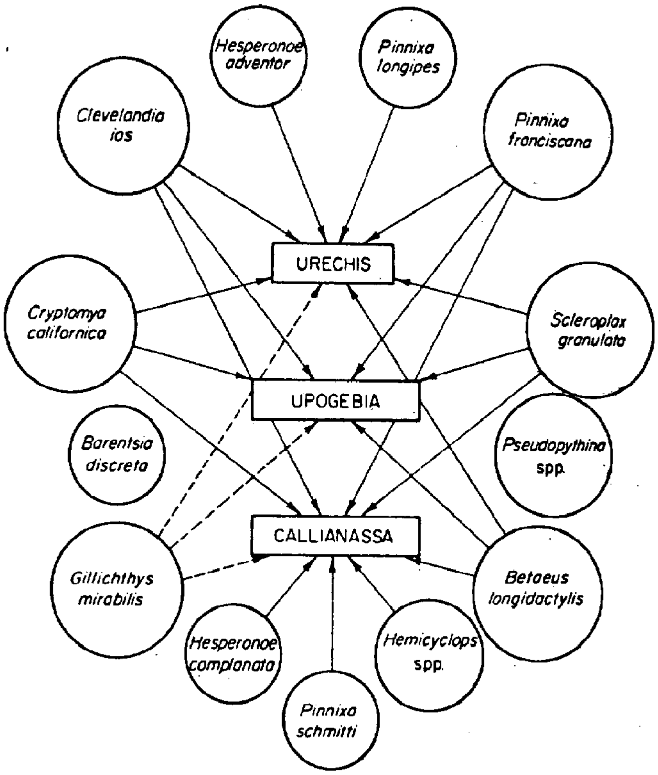

Hesperonoe adventor
Pinnixa longipes
Clevelandia ios
Pinnixa franciscana
URECHIS
Cryptomya californica
Scleroplax granulata
UPOGEBIA
Barentsia discreta
Pseudopythina spp.
CALLIANASSA
Gillichthys mirabilis
Betaeus longidactylis
Hesperonoe complanata
Hemicyclops spp.
Pinnixa schmitti

Fig. 46: Commensals of the echiuroid, Urechis and the burrowing crustaceans, Upogebia and Callianassa (From Dales 1966; Fig. 4)

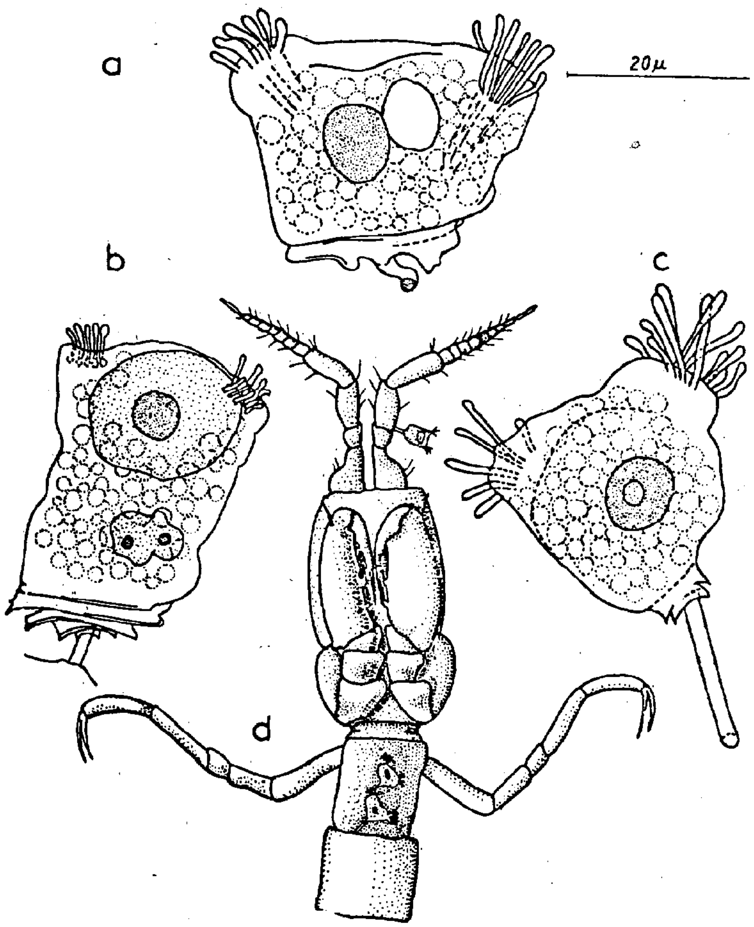


Fig. 47: Commensal suctorians (Tokophyra microcerberi Delamare and Chappuis) on the amphipod Microcerberus remyi Chappuis (After Delamare and Chappuis, from Delamare 1960; Fig. 254).

coast, the fauna is becoming fairly well known and the distribution patterns of some key groups have been studied. Species relations are only beginning to be clarified under laboratory conditions. It may, therefore, be too early to predict the degree of species correlation which will eventually be shown to characterize the sandy beach. However, the high energy beach is a geomorphological entity and presumably a biological entity as well, with a multitude of interlocking and homeostatically functioning components, protected, or at least delimited, from neighboring systems. One group of such interconnecting components is based on interspecific relations. Others are based on common food sources, general edaphic structures and/or common gradients of key climatic factors all integrated by geomorphological features. At least one of the causes underlying species correlation must be strong, if even moderate homogeneity is to occur. Since most of the physical patterns which give rise to high energy beaches are strict and rigorous, and probably dominate the system, interspecific relations may play a relatively small role in keeping the system in order and functioning.

Dynamics of the High Energy Beach System

Just as the existence of each organism is based on a permanent flow, interchange and exchange of energy, substances, and structures, so does the existence of each ecosystem depend on their balanced flow. This analogy should not be exaggerated, but clearly an ecological unit must obey the laws of its living components, as well as the laws governing its entity as a balanced system.

Permanent trophic dynamics

Not only should the lines and loops of the food chains be followed through the individual producer, consumer, and decomposer steps, but the whole balance between input and output should be examined.

Primary producers, autotrophic plants, are restricted to microscopic, interstitial groups, mainly diatoms. In sheltered areas, this benthic plant life may be dense, but it is restricted to the top centimeter (Pomeroy 1959) and tends to migrate to the surface (Aleem 1950). In high energy beaches, however, the diatom population is scarce (20g C/m^2) and the yearly production is very low (4-9g C/m^2). These organisms may extend down to 20 cm, however, (Steele and Baird 1968), and this raises two main questions.

First, since mixing of sand over long periods affects no more than the top 5 to 10 cm, populations below this level have no access to light for several months. One might assume that these diatoms assimilate carbon heterotrophically (Lewin and Lewin 1960), but to other authors (Munro and Brock 1969) this seems unlikely. Second, it is obvious that the small productivity within the system does not cover the system's general needs. Thus, other stronger food sources bringing energy from outside can be predicted.

Among the consumers, there are only a few groups of macrofauna which contribute energy to the system by collecting food from outside. One type of endofauna collects food outside and releases feces within the substratum (Emerita, Amphioxus); a second type collects outside but also releases wastes outside (Cardium, Donax); a third type filters particles from the sand and deposits feces on the surface (Arenicola, Balanoglossus). The contribution of these macro-organisms may be considerable, but little data are available. The contribution of the filtering mesofauna seems not to count quantitatively, nor is it clear how much they really take from outside the system.

The largest percentage of the psammon species feed within the sediment layers themselves. Remane (1952; see Fig. 48) shows the high diversity of feeding types. However, the participation of several other groups such as heterotrophic or saprophytic plants has not yet been evaluated. There is evidence that bluegreen algae reach a density of 10,000 cells per liter of sediment in the deeper layers, equal to the maxima of nematodes (Riedl, unpublished), but their contribution to or position in the food chain is unknown.

Undoubtedly, the decomposers have a key position in the beach system, due to their density and their variety of functions. Humm (in Pearse et al. 1942) counted 200,000 bacteria per gram of sediment belonging mainly to the nitrogen cycle, agar- and chitin-digestion groups. Besides these, the sulfur bacteria (Fig. 49) are of great importance, particularly in the black layer. Altogether 16 different functions of bacteria within the sediment are listed (ZoBell 1938). Decomposers in the sand environment obviously represents also an important food source for a great number of consumers. Whole phyla might be specialized on them.

The energy input and output relationships of the beach system - all the correlations with neighboring environments - are still unsolved. A great energy input is to be expected from the open sea, but wrack beds, birds, and groundwater flow also contribute energy to the system. Adequate data are lacking.

It has been generally assumed that detritus and plankton washed up on the beach may be one of the main food sources of the psammon. Yet cadavers of planktonic organisms are seldom found within the porous system and only the smallest types of phytoplankton can fit into the interstices. In contrast to this, the content of organic matter may be remarkably high. The senior author therefore suggests a theory of a "beach-filter-mechanism", as follows.

First, dissolved organic matter in sea water ranges mostly between 0.5 and 2.5 g carbon per ton and the values are especially high in surface and coastal waters. Second, bubbling air through a seawater column creates foam at the surface, the amount of which corresponds to particulate matter produced, which may be a food source for invertebrates (experiments with sea-aquarium techniques and experimental oceanography, Sutcliffe, Baylor and Menzel 1963, Barber 1966, and others; for criticism see Menzel 1966). Third, the surf may be considered as a permanent and effective bubble mechanism, extremely fine bubbles reaching a depth of thirty meters (Riedl 1966). Fourth, within the whole critical depth, the oscillation of water particles underneath the waves reaches the bottom. Thus, not only does the foreshore region receive strong input from each wave, but a large part of the offshore region must also be included. In the foreshore region gravity contributes to the penetration of surfwater into the sand-body. In the offshore region mixing of water with the sediment surface layer is important. Also the suction effect of the boundary

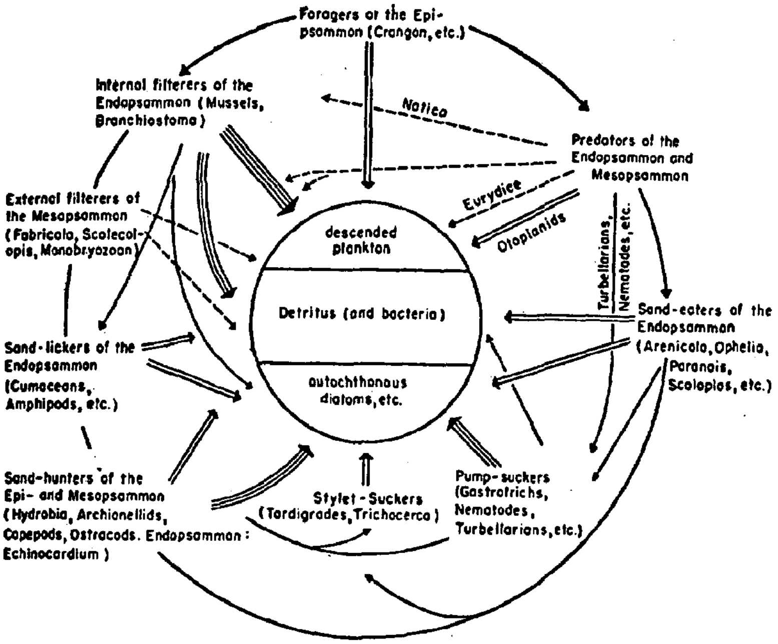

Foragers of the Epi-psammon (Crangon, etc.)
Internal filterers of the Endopsammon (Mussels, Branchiostoma)
Natica
Predators of the Endopsammon and Mesopsammon
Eurydice
Otoplanids
External filterers of the Mesopsammon (Fabricola, Scolecolepis, Monobryozoon)
descended plankton
Detritus (and bacteria)
autochthonous diatoms, etc.
Turbellarians, Nematodes, etc.
Sand-eaters of the Endopsammon (Arenicola, Ophelia, Paranois, Scoloplos, etc.)
Sand-lickers of the Endopsammon (Cumaceans, Amphipods, etc.)
Sand-hunters of the Epi- and Mesopsammon (Hydrobia, Archianellids, Copepods, Ostracods. Endopsammon: Echinocardium)
Stylet-Suckers (Tardigrades, Trichocerca)
Pump-suckers (Gastrotrichs, Nematodes, Turbellarians, etc.)

Fig. 48: Diagram of feeding relationships of the sand fauna (After Remane, from Hedgpeth 1957b; Fig. 7).

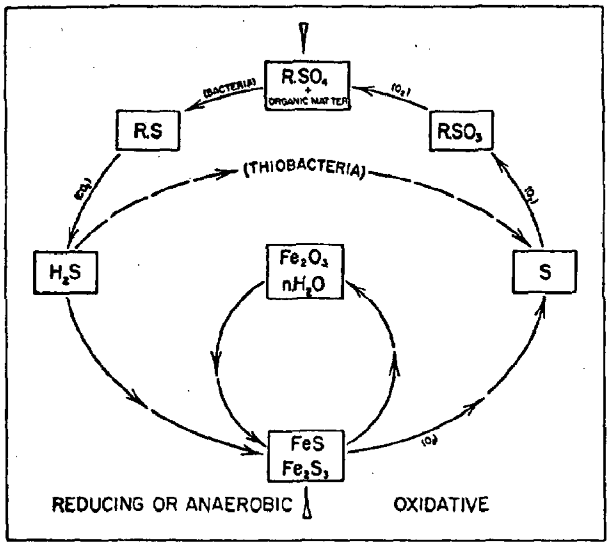

R.SO4 + ORGANIC MATTER
(BACTERIA)
(O2)
R.S
RSO3
(THIOBACTERIA)
(O2)
(O2)
H2S
Fe2O3 nH2O
S
FeS Fe2S3
(O)
REDUCING OR ANAEROBIC
OXIDATIVE

Fig. 49: Sulfur cycle in a marine beach (After Bruce, from Hedgpeth 1957b; Fig. 5).

layer, migrating with the permanent translocation of the pattern of particle speed near the bottom may cause a flow through the interstices from locations of minima to maxima of oscillation velocity. Within the sandripple structure this suction pattern may even become stable. Fifth, finer fractions of the sediment attract very small particles and possibly even the most extremely fine particulate matter. Theoretically, these five components together form the world's largest physical filter of organic matter.

Only theories are available with regard to input problems, but even more obscure are the phenomena relating to output of the biological beach system. Very few live adults or larvae of the psammon may be expected to leave the sand environment, so CO_2 and nutrients may be the main contribution of the sandy shore to the overall marine biosphere.

Rhythmical changes

As in most coastal environments, rhythms are strong. They control population fluctuations, faunal distribution, and physiology as well as variations in behavior. Three main types of rhythms can be distinguished according to their length and the causal forces involved. They influence each other.

Tidal rhythms change the energy pattern, humidity, interstitial oxygen (Fig.50) groundwater flow and other parameters. The epipsammon follow exactly the translocation of the shoreline with the tides. Many groups of the endopsammon do also. Emerita (MacGinitie 1938, Pearse et al. 1942) and Donax (Fig.52, Mori 1938, Marsh 1962) are good examples. Within the mesofauna the earliest case reported was Convoluta roscoffensis (turbellarians; Gamble and Keeble 1903) which appears in masses during low tide, forming green patches on the sediment surface and exposing their symbiotic algae to the sunlight. Most behavioral adaptations to the tidal rhythms may be still undiscovered. However, it was shown recently (Rieger and Ott 1968) that five types of migratory patterns can be observed: active vertical migration with the tide, active vertical migration against the tide, active horizontal migration at low tide, passive migration with the tide (riding on drifted shell), and mixed types of migration.

Circadian (daily) rhythms change visibility and surface conditions within the back and foreshore areas. Shorebirds are active in the daytime, while ghost crabs and egg-laying seaturtles appear at night. Convoluta appears at low tide only during daylight hours and some behavioral patterns of vertical migrators (mentioned above) are under a circadian regime, due to loss of humidity and raising of temperatures during strong radiation.

Seasonal changes are due mainly to the influence of water and air temperature directly, and indirectly through their effect on other parameters such as oxygen (See Figs. 7,8,9,51 and Table 1,2,3,6,7). Growth, activity, breeding and many other processes are seasonally directed and nearly all species within the system are affected. Furthermore migration and density of populations are related to seasons. Populations of one of the typical intertidal amphipod species decrease in winter and move seaward (Dexter 1967); the same is true for an intertidal turbellarian (Dörjes 1968; Fig. 53). The opposite holds for some moist zone tardigrades which approach the shore, with a minimum population in summer (DeZio and Grimaldi 1966).

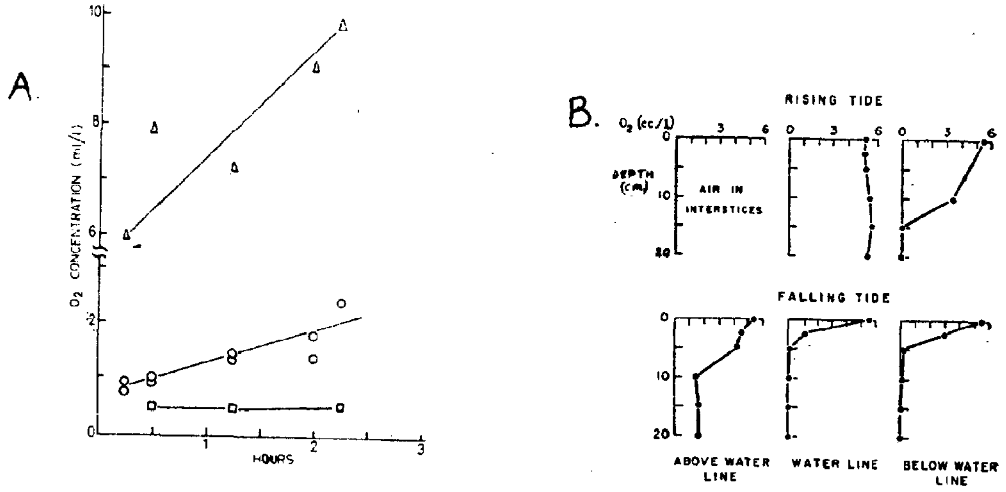


Fig. 50: Change in oxygen concentration in interstitial water. A. according to length of time that site (Whitstable, England) was exposed by the tide. Triangles represent surface water; circles, interstitial water at 2 cm depth; squares, interstitial water at 5 cm depth (After Brafield 1964; Fig. 5). B. during rising and falling tides (Corona del Mar, California) (From Gordon 1960; Fig. 1).

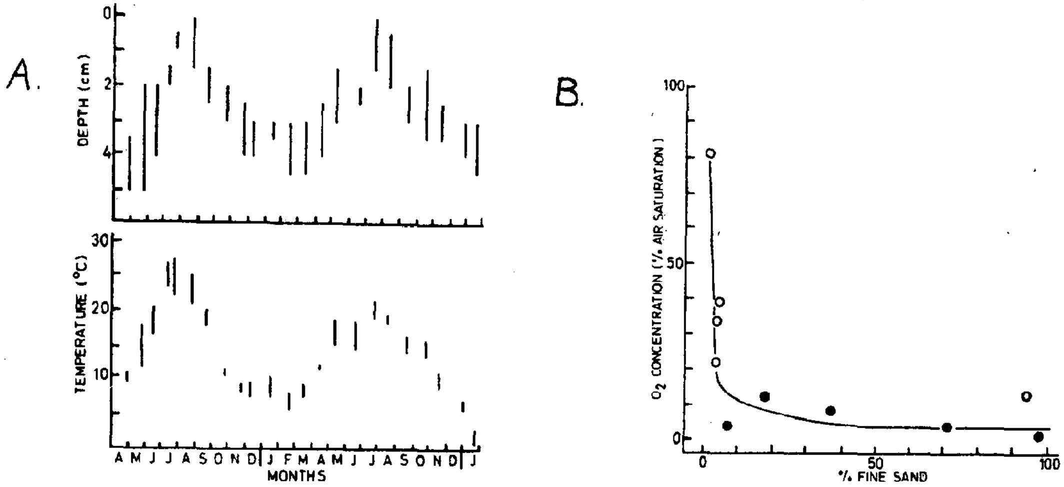


Fig. 51: Relationship of anaerobic black layer to depth and fine sand. A. variation of black layer with depth and temperature at Whitstable, England over a period of 22 months. B. relationship between oxygen concentration of the interstitial water and percentage of fine sand in the substrate samples, Isles of Scilly. Solid circles indicate black layer (Gordon 1960).

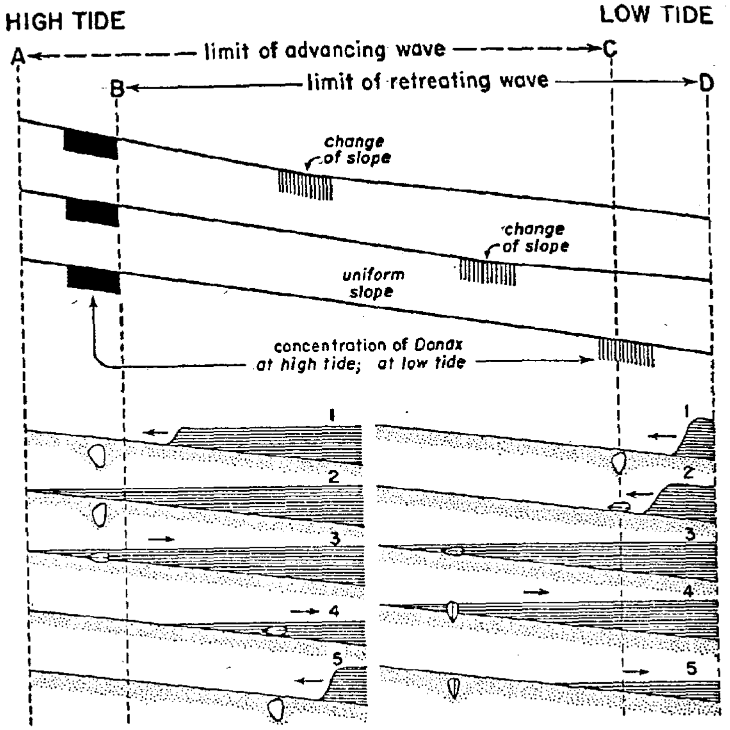

HIGH TIDE
LOW TIDE
A
limit of advancing wave
C
B
limit of retreating wave
D
change of slope
change of slope
uniform slope
concentration of Donax at high tide; at low tide
1
2
3
4
5
1
2
3
4
5

Fig. 52: Relations of *Donax* to beach slops (above) and their method of migrating with the tide (below); left, on a falling tide; right on a rising tide (Compiled from Mori; from Hedgpeth 1957b; Fig. 9).

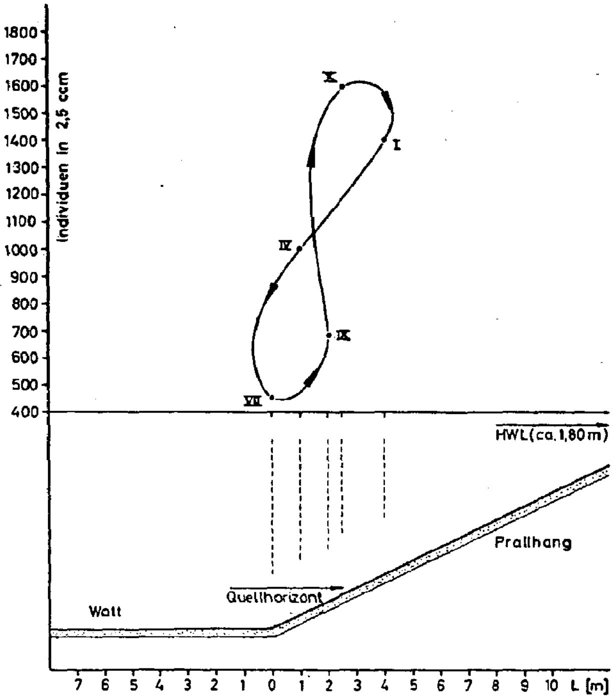


Fig. 53: Annual migrating and density pattern of the turbellarian *Haplogonaria syltensis* in the well horizon. Roman numerals indicate the monthly maxima for five months (From Dörjes 1968; Fig. 15).

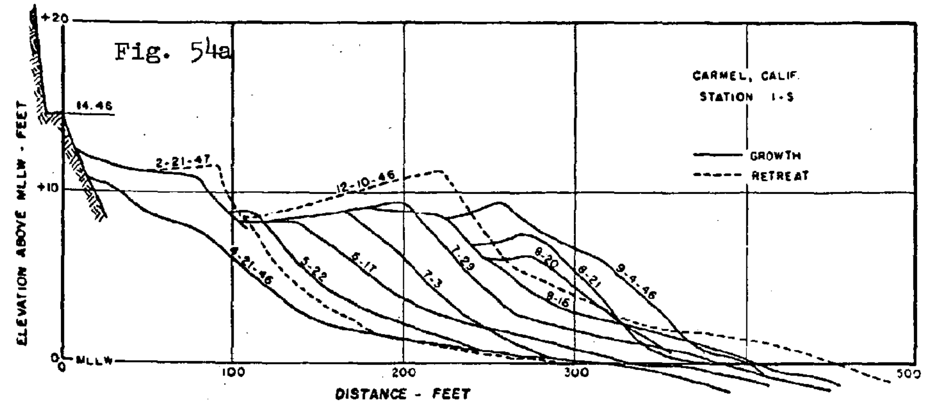
Mixed types which are dependant on more than one of these rhythms might be expected to be rather abundant, but clear examples are difficult to find. Convoluta has been mentioned. One of the most striking examples is in the macrofauna, an atherinid fish, the grunion, (Leucresthes; Clark 1925, Korringa 1957). It spawns during a 1 to 3 hour period in summer leaving the water at night immediately after spring hightide. On such a night the exposed part of the foreshore may be covered with mating and egg-depositing specimens. Developing eggs buried in the sand, are designed to be protected a fortnight and to be washed back to the sea with the following spring tide.

Biological successions in high energy beaches, non rhythmical and often non reversable, vary greatly in their time scale. They range from intervals of an hour to geological times; from the time it takes to conquer a new microniche to the lifetime of the shelf system of a continent. Within short intervals, direct observations are possible, while long time effects can only be derived.

In short term succession, it would be interesting to know the time required and the processes involved in the conquest of new substrata, in the balancing of communities and in community aging and disappearance. Only a few of these problems have been touched however. Sterilized sand put back on the beach becomes repopulated rapidly and its biological balance is reached in a short time (Boaden 1962). This is understandable because all the biotic elements are very near and ready to expand into the new space. Yet very isolated sands are also populated in a relatively short time: A seacave within the steep rock of Banjole (northern Adriatic; Riedl 1966 p. 59) contained no sand from 1952 to 1964. Boulders appeared in 1961 in its background and were undergoing grinding in 1962; coarse sand and shell with ripplemarks were produced in 1964. In 1965 and 1966 this sediment had already assembled otoplanids (Riedl unpublished). Yet the nearest environment with otoplanids was two miles away on the shore. Unfortunately, nothing is known regarding the processes or the time required for ripening or ageing the sand biome.

Long time successional effects are related to permanent change in the beach profile and the whole coastline. Large amounts of surface sand are transported daily and the profile of the beach changes with wave action. Often retreat of sand produces large cuts (Bascom 1951; Fig. 54A) and sand accretion occurs in smaller steps. Biologically this means that in an eroded area either most of the sand fauna are lost or they have mechanisms to protect themselves such as by hiding in deeper layers. It also means that vertical zonation and layering must change daily. As a matter of fact, nearly all species tend to migrate, even the smallest types within the interstitial spaces. The tardigrades migrate up to a foot a day (DeZio and Grimaldi 1966; Fig. 55). Everything is in motion in the sand, and a specimen may never reencounter its place of birth.

In places with high sediment output and strong waves and currents, as in inlets of estuaries (Fig. 54B), coastal lines change dramatically. In cases such as Aveiro, Portugal, where data over long historical periods are available (since 1318, according to Abecasis 1955) changes of beachlines are especially striking. And on the geologic time scale, we need go only into early Pleistocene to see changes in continental dimensions. It is evident that the psammon have easily followed all the physical translocations of sandy beaches, the most movable part of this ancient system.



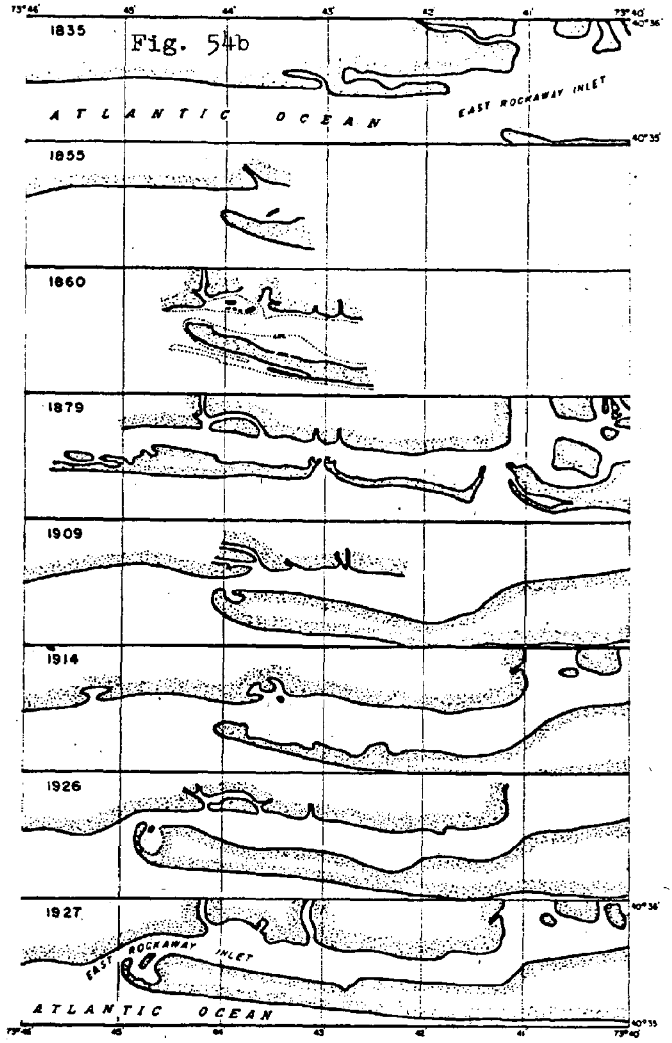


Fig. 54b
73°44'
45'
44'
43'
42'
41'
73°40'
40°36'
40°35'
1835
ATLANTIC OCEAN
EAST ROCKAWAY INLET
1855
1860
1879
1909
1914
1926
1927
EAST ROCKAWAY INLET
ATLANTIC OCEAN

Fig. 54: Deposition and erosion of exposed beaches. A. at Carmel California over a period of several months (After Bascom); B. at East Rockaway Inlet, N.Y. (After U.S. Army) (From Wiegel 1964; Figs. 14.24, 14.35).

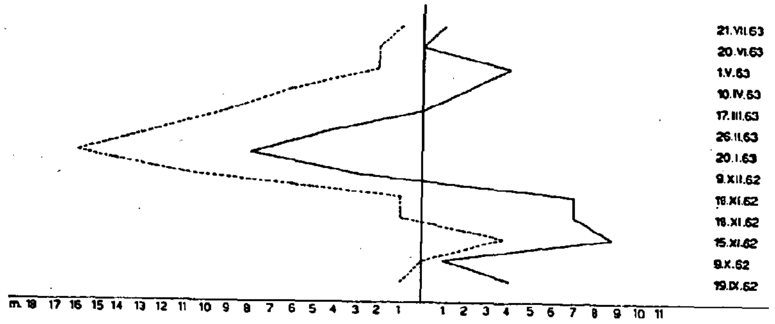


Fig. 55: Shoreline displacements (unbroken line) and highest frequencies of Tardigrada (broken line) relative to the average shoreline for a one year period (From de Zio and Grimaldi 1966; Fig. 4).

Chapter A-3

HIGH VELOCITY ECOSYSTEMS

In channels where sea waters flow at high velocities, 3 to 20 miles per hour or more, bottoms are swept clean of fine sediments and reef-like accumulations, and specialized encrusting organisms develop growths, taking advantage of the foods available in the rapidly passing waters. The same kinds of ecosystems also develop on the bottoms of ships where they are sometimes called "fouling communities" and inside large pipes through which sea waters are pumped as in industries where waters are used for cooling. In nature the system occurs on hard coarse bottoms where tidal flow passes through narrow passages and inlets.

The very strong current dominates the system and allows dense patterns of attached organisms but also is a source of stress requiring energies to be expended by the organisms in adaptation. If the surface is within range of light, heavy algal growths develop facilitated by the rapid renewal of nutrients for photosynthesis. High velocity channels are favorite collection locations for dredging of marine organisms in quantity. Because the high currents often occur in high salinities at the entrance to estuaries where conditions, other than current, are uniform, species diversities tend to be moderately high, but diminishing with current. This system is found in every state of the U.S. but one of the best studied examples comes from abroad.

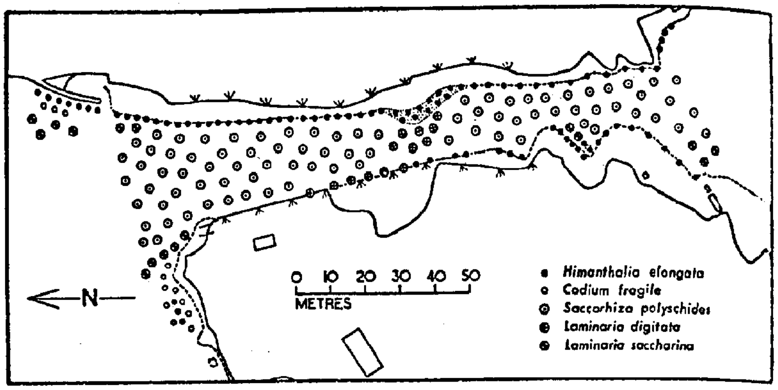
EXAMPLES

Lough Ine Rapids

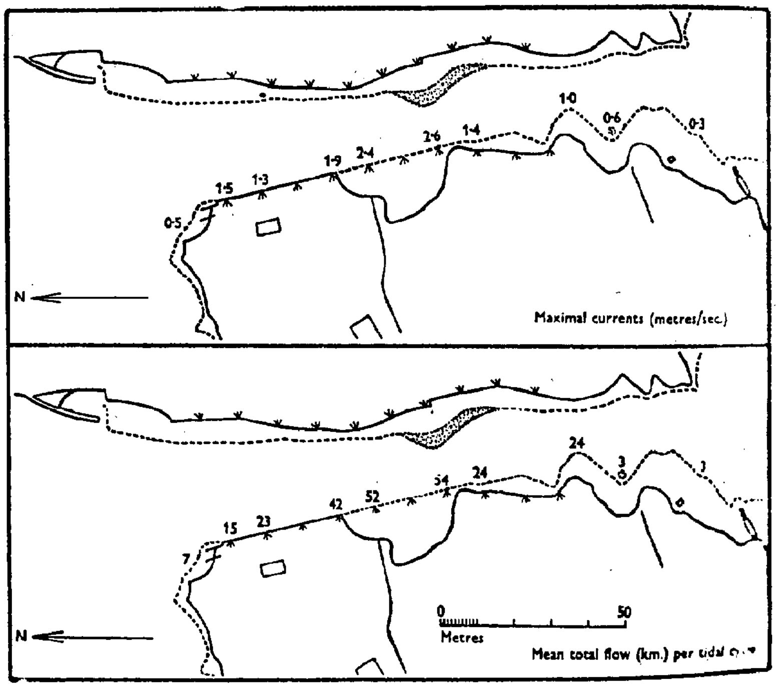
A much studied ecosystem is the Lough Ine Rapids in Scotland where a strong tide flows in and out of a Scottish loch forming a shallow salt water rapids in which grows an enormous concentration of plants and animals as illustrated in Figs. 1-4, taken from a recent review article of these studies (Kitching and Ebling, 1967). Heavy growth of algae supports a food chain of algae-eating sea urchins (Paracentrotus). Laminarian brown algae grow in other zones, supporting encrusting bryozoa with densities that vary with the current (Fig. 4). Invading with different stages of the tide and time of day are crabs and fishes that eat animals from the rich bottoms when slack currents permit (Figs. 2 and 3).

Worm Tube Reef in a Cooling Intake Pipe

Heavy calcareous reefs built by animals in the pipes of fast flowing salt waters occur in the intake of the Corpus Christi Power and Light Company, Texas (Behrens, 1968). The growth rapidly closes the pipe unless prevented (partly) with chlorination. The waters drawn into the pipe come from a polluted harbor, which may account for the simplicity of the worm tube reef, exclusively of Hydroides norvegica Gunnerus. This serpulid is also found on the bottoms of ships that enter the harbor (Fig. 5). The larvae are released into bay waters (Fig. 6). Other cooling pipes have simple reefs of other species. Hutchins found mussels forming reefs (10 lbs per square foot in 4 months) in cooling pipes in Massachusetts (Woods Hole Oceanographic Institution, 1952a). The problem of reefs in pipe may be very serious. If chlorination is used to kill intake organisms, the system

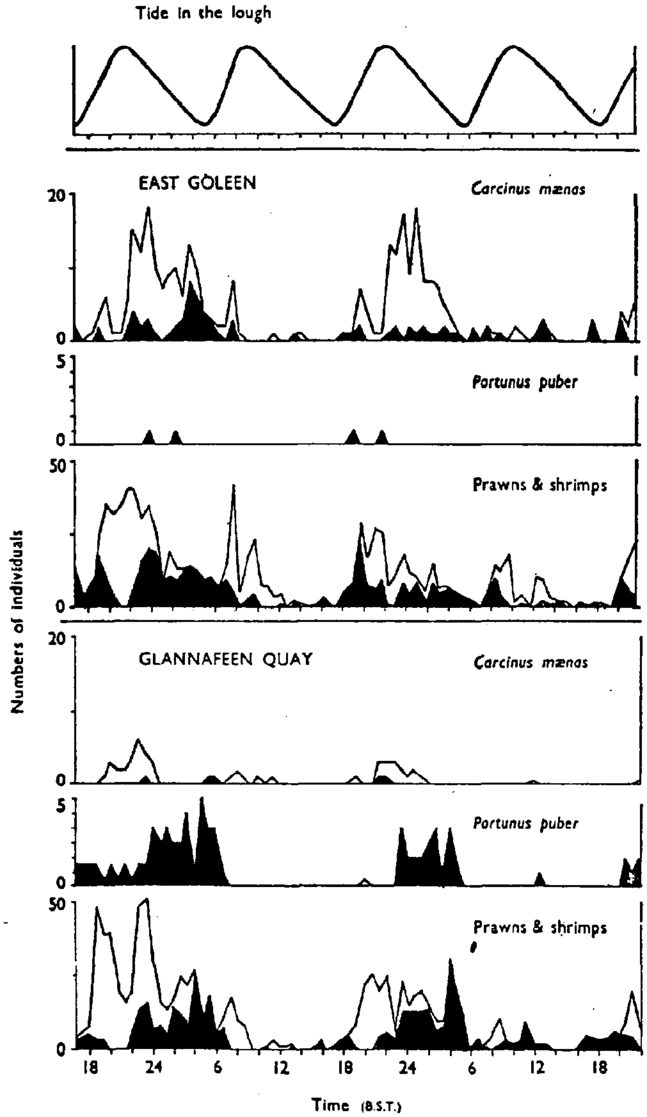

N
0 10 20 30 40 50
METRES
● Himanthalia elongata
○ Codium fragile
◎ Saccorhiza polyschides
● Laminaria digitata
● Laminaria saccharina

The distribution of dominant sublittoral algae in the Lough Ine Rapids in September 1946. The *Codium fragile* is subsp. *tomentosoides*.


1·0
0·6
0·3
2·6
1·4
1·9
2·4
1·3
1·5
0·5
N
Maximal currents (metres/sec.)
24
3
3
54
24
42
52
15
23
7
N
0
50
Metres
Mean total flow (km.) per tidal cycle

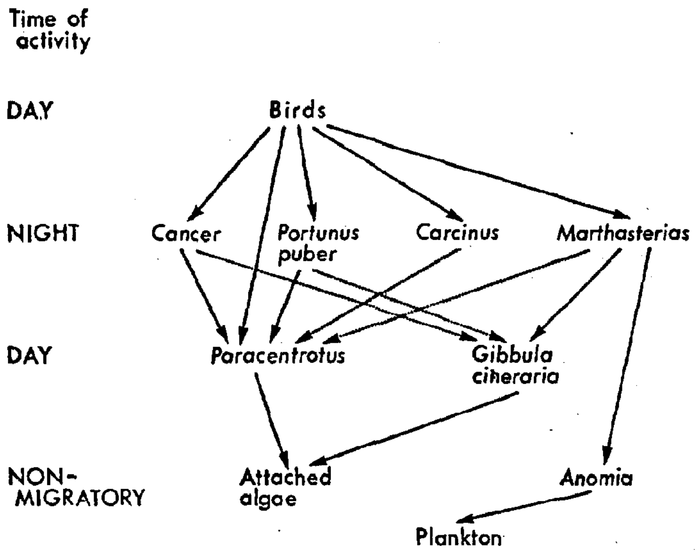
Water currents at level of the canopy. (a) Maximal currents in metres per sec.; (b) Mean total flow in kilometres per tidal cycle (based on average of figures for spring and neap tides.)

Fig. 1. A salt water tidal rapids in Scotland (Kitching and Ebling, 1967).



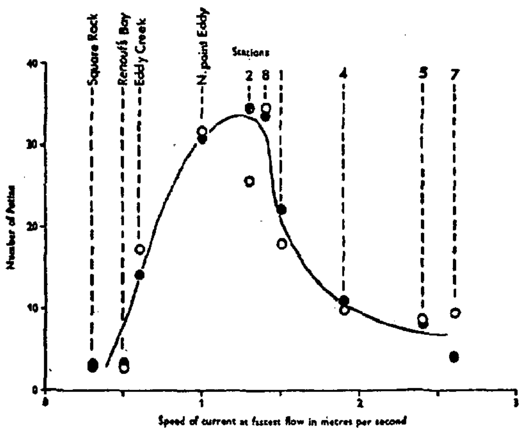
Numbers of crabs and prawns on beds of small mussels laid in extreme shelter at East Goleen, and in a more open part of the Lough at Glannafeen Quay. Black signifies sublittoral, white signifies littoral. *Carcinus maenas* and *Portunus puber* were opening and eating the mussels; the prawns (mainly *Leander serratus*) were merely scavenging.

Fig. 2. Swimming carnivores in the Lough Ine Rapids (Kitching and Ebling, 1967).


Time of activity
DAY
Birds
NIGHT
Cancer
Portunus puber
Carcinus
Marthasterias
DAY
Paracentrotus
Gibbula cineraria
NON-MIGRATORY
Attached algae
Anomia
Plankton

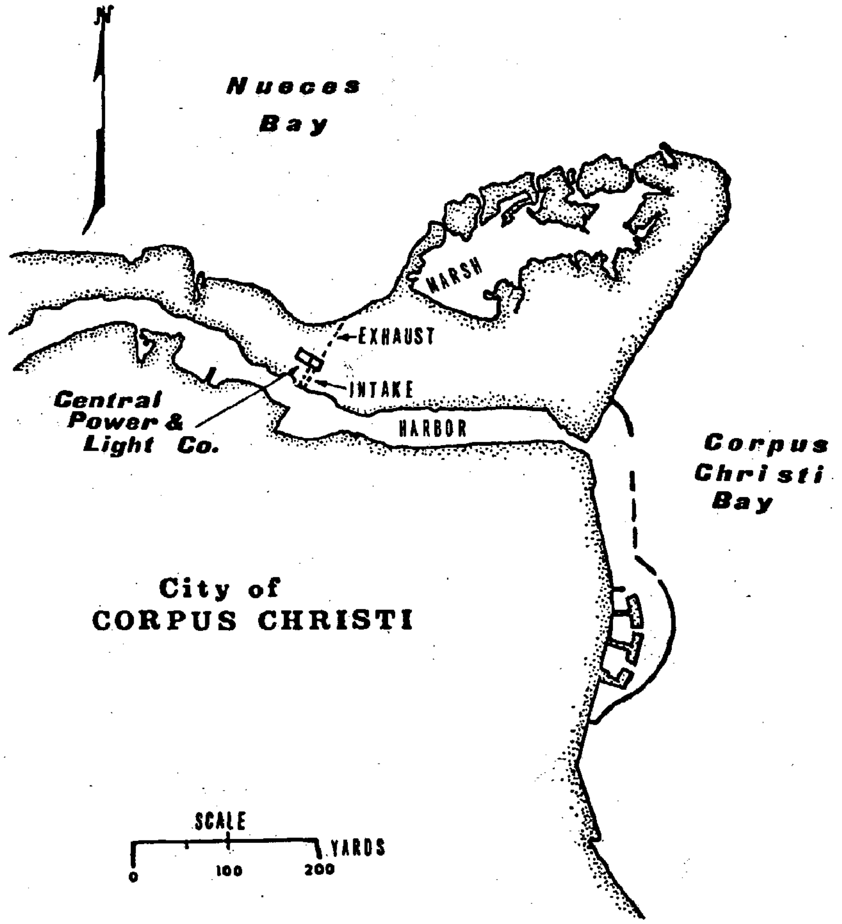
Diagrammatic representation of major food chains in the *Paracentrotus* community in relation to times of daily activity.

Fig. 3. Urchin-algae food chain in Lough Ine Rapids (Kitching and Ebling, 1967).



Population density of *Patina pellucida* on *Saccorhiza polyschides* (whole plant) in relation to the speed of current at fastest flow (in metres per second). For position of stations see Fig. 4. September 1946. ● mean number of *Patina* per *Saccorhiza* plant; ○ number of Patina per 3 lb of *Saccorhiza*.

Fig. 4. Populations and current velocity in the Lough Ine Rapids (Kitching and Ebling, 1967).


N
Nueces Bay
MARSH
EXHAUST
INTAKE
HARBOR
Central Power & Light Co.
Corpus Christi Bay
City of CORPUS CHRISTI
SCALE
0
100
200
YARDS

Location map showing the cooling water intake tunnels on the North side of the harbor of the city of Corpus Christi, Texas.

Fig. 5. Site of worm tube reef in cooling intake pipe in Texas (Behrens, 1968)

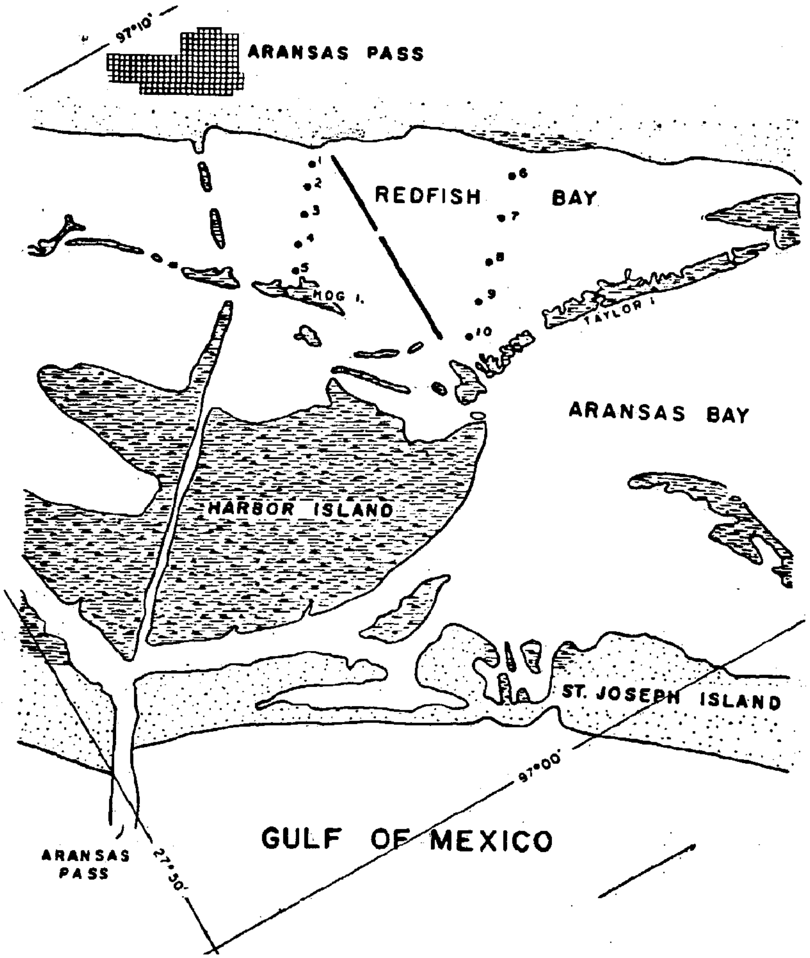

97°10'
ARANSAS PASS
REDFISH BAY
1
2
3
4
5
6
7
8
9
10
HOG I.
TAYLOR I.
ARANSAS BAY
HARBOR ISLAND
ST. JOSEPH ISLAND
97°00'
GULF OF MEXICO
ARANSAS PASS
27°50'

Fig. 7. Map showing Aransas Pass inlet with jetties

will serve to deplete bays of larvae, foods, and biotic food chains to whatever extent the bay waters are pumped.

Aransas Pass Inlet

Aransas Pass (Fig. 7) is one of the many narrow inlets through which main currents of estuarine exchange flow in and out of the open sea. Dredging in this inlet produces coarse rubble of encrusting reef animals including sponges, oysters, bryozoa, barnacles, mussels, and other filter feeding animals. The seasonal pattern of larval release from reef-forming animals in the inlet is given by Behrens (1968) in Fig. 6. Other data are in Fig. 8. One of the carnivores of the rocky margins is the stone crab which can break open encrusting skeletons. Powell and Gunter (1968) (Table 1) found seasonal changes in sizes. Black Abalones from California were introduced in the pass in December 1959. They lived on the rocks until high temperatures of summer.

Beaufort Inlet, N.C.

With higher tides than at Port Aransas, a wider channel is maintained at Beaufort Inlet, N.C. (Fig. 9A) strong currents being spread over a wider zone. Ingram (1965), as shown in Fig. 9B, maps coarse sediments of shell and sand with little residual organic matter. The fast and turbulent injections of waters from estuarine and open sea sides alternate with the tides, most plankton being recently injected from less stirred areas and removed from the inlet before any kind of adaptation may take place. These plankton populations, however, are the basis for rapid growths of attached animals on sides and bottoms.

Williams and Murdoch (1966d) (Fig. 9A) measured weight of plankton, chlorophyll representing phytoplankton, and bottle measurements of photosynthesis and respiration serving as an indication of the physiological state of the cells. The seasonal pattern of larval release and setting mainly runs with the pulse of available plankton production, March to November, as given in Fig. 10 (Woods Hole Oceanographic Institution, 1952a).

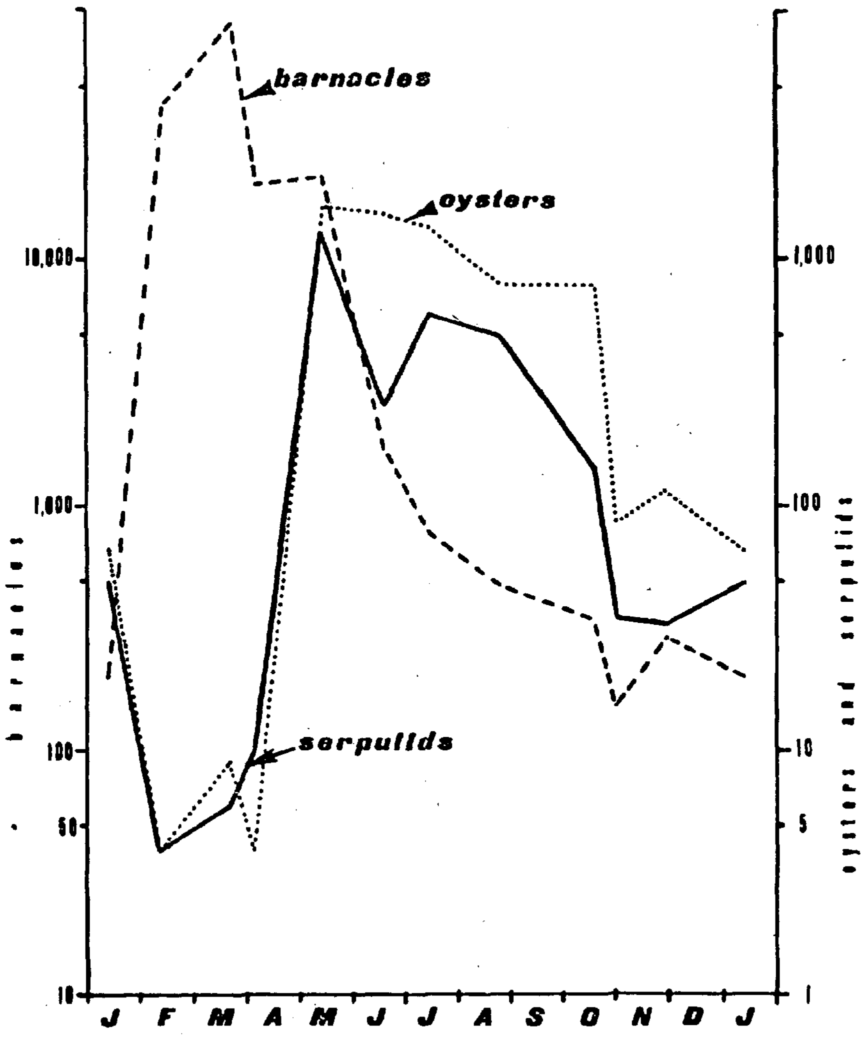
Rollover Pass, Texas

A much studied inlet in Texas is Rollover Pass shown in Fig. 11. Probably because nearby Galveston inlet (Bolivar) was deepened for navigation, sediment filled in the small natural pass. At the behest of sportsmen it was dredged open in 1955 (300-1800 ft wide), although it soon filled up again. While open it was a popular fishing location and Reid (1957) studied the fishes before and after the changes, describing the inlet as faunistically rich with speckled trout, croaker, spadefish, drum, redfish, pigfish, silver perch, pinfish, ladyfish, catfish, rays, sharks, bluecrabs, eels, and pompano.

The Floating Buoy

Buoys are anchored in channels and inlets and have very fast current regimes with rapid growth of the attached ecological system. In Table 2 and Fig. 13 are shown the weights which accumulate, these in addition to the export of growth to the many animals that feed on these reef-like accumulations.

In Fig. 12 is shown a much quoted diagram of the early start of succession with the bacteria making an immediate slime covering followed by algae (if



Numbers of larvae of the three most abundant fouling organisms settling and metamorphosing on filter screens in flowing sea water system at the University of Texas Marine Science Pier Laboratory on Aransas Pass inlet, Port Aransas, Texas.

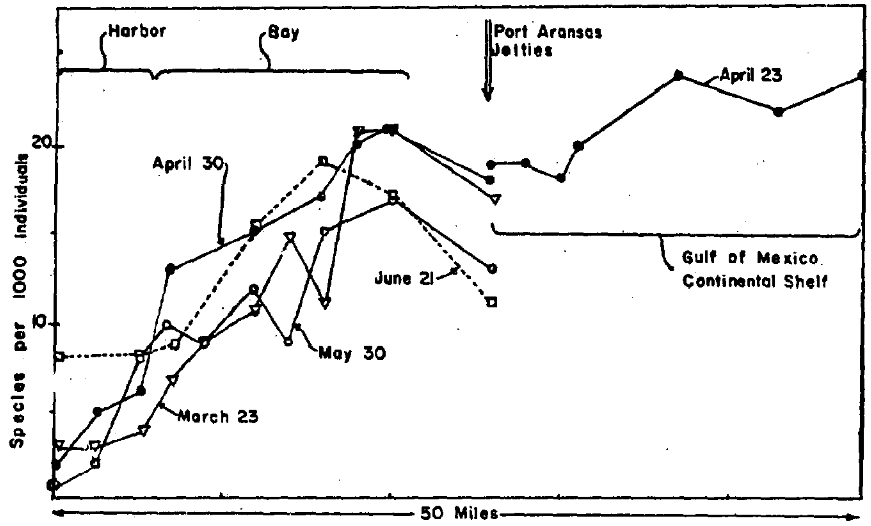
Fig. 6. Larval set in Aransas Pass Inlet, Texas (Behrens, 1968)

Table 1.

Measurements in millimeters of stone crabs taken from the south jetty (Mustang Island) of Aransas Pass.
(1947-48)

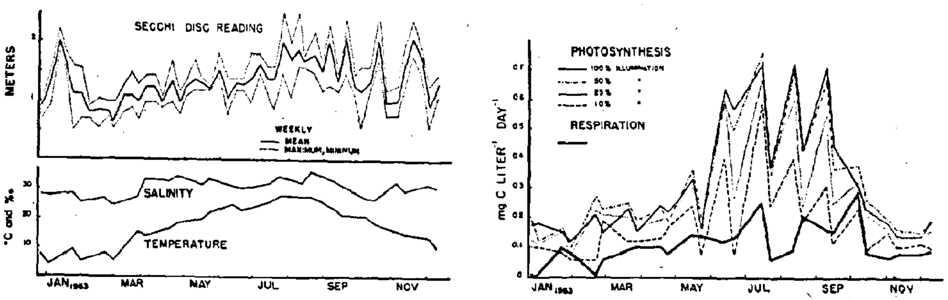
	December	January	June	July	August
Number	10	45	71	73	95
Range, Width of Carapace	9.8 to 17.1	5.5 to 49.0	4.2 to 74.6	3.9 to 80.0	4.8 to 62.4
Mean Width of Carapace	12.32	22.53	24.97	29.95	24.74

(Powell and Gunter, 1968)



Species diversities in zooplankton (species per thousand individuals) from the western end of Corpus Christi Harbor to a station 25 miles out on the shelf of the Gulf of Mexico off Port Aransas.

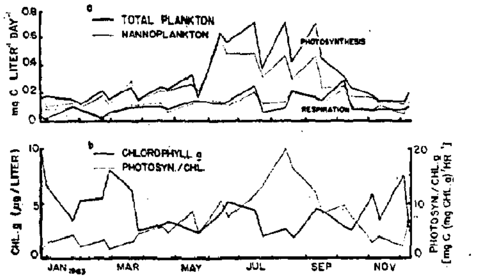
Fig. 8. Diminished diversity in the mixing zone of bay and shelf through jetties in Texas (Odum, Cuzon, Beyers, and Allbaugh, 1963).



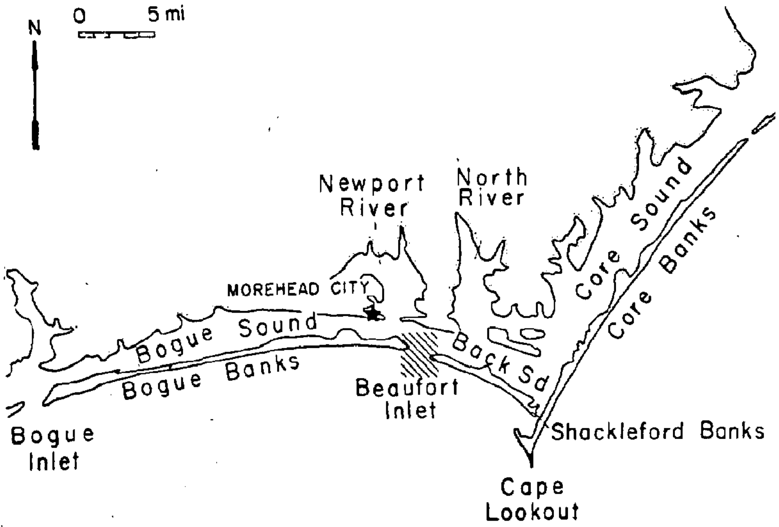
Secchi disc reading, salinity, and water temperature.

Gross photosynthesis and respiration at four light levels.

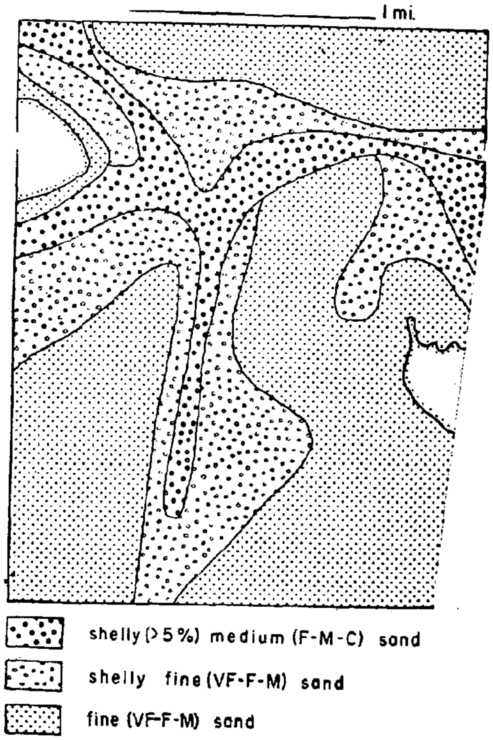
Fig. 9A. Characteristics of water, phytoplankton, and productivity in Beaufort Inlet, N.C. (Williams and Murdoch, 1966d).



a. Gross photosynthesis at surface illumination and respiration of total plankton and of nannoplankton alone. *b.* Chlorophyll *a* concentration and the ratio of the average rate of gross photosynthesis during the daylight hours at surface illumination to chlorophyll *a* concentration.

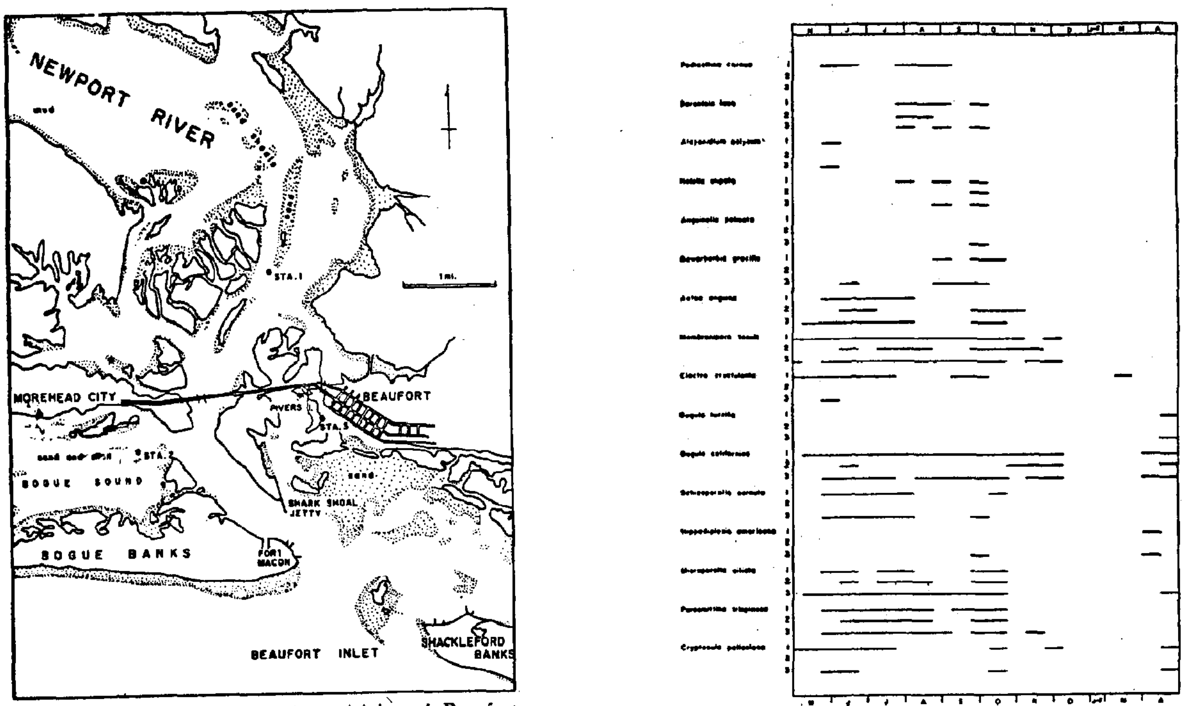

N
0
5 mi
Newport River
North River
MOREHEAD CITY
Bogue Sound
Bogue Banks
Beaufort Inlet
Back Sd
Core Sound
Core Banks
Shackleford Banks
Bogue Inlet
Cape Lookout

–Index Map. Ruled area shows location of region covered by figures


1 mi.
shelly (>5%) medium (F-M-C) sand
shelly fine (VF-F-M) sand
fine (VF-F-M) sand

–Gross lithology of Beaufort Inlet

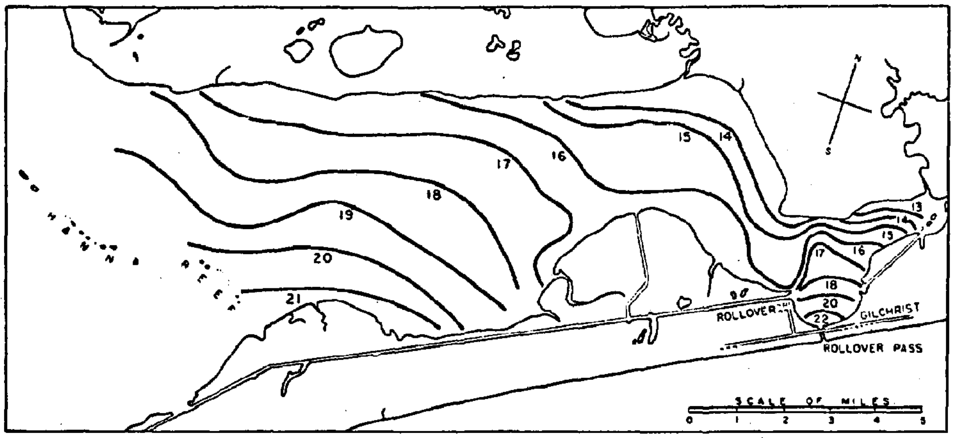
Fig. 9B. Sediment characteristics in Beaufort Inlet, N.C. (Ingram, 1965).


NEWPORT RIVER
MOREHEAD CITY
BEAUFORT
RIVERS
STA. 1
STA. 2
STA. 3
1 MI.
BOGUE SOUND
BOGUE BANKS
SHARK SHOAL JETTY
FORT MACON
sand
BEAUFORT INLET
SHACKLEFORD BANKS
M J J A S O N D J-F M A
1954
1955

Map of the immediate vicinity of Beaufort, North Carolina, with the locations of the three stations and notations on the bottom types.

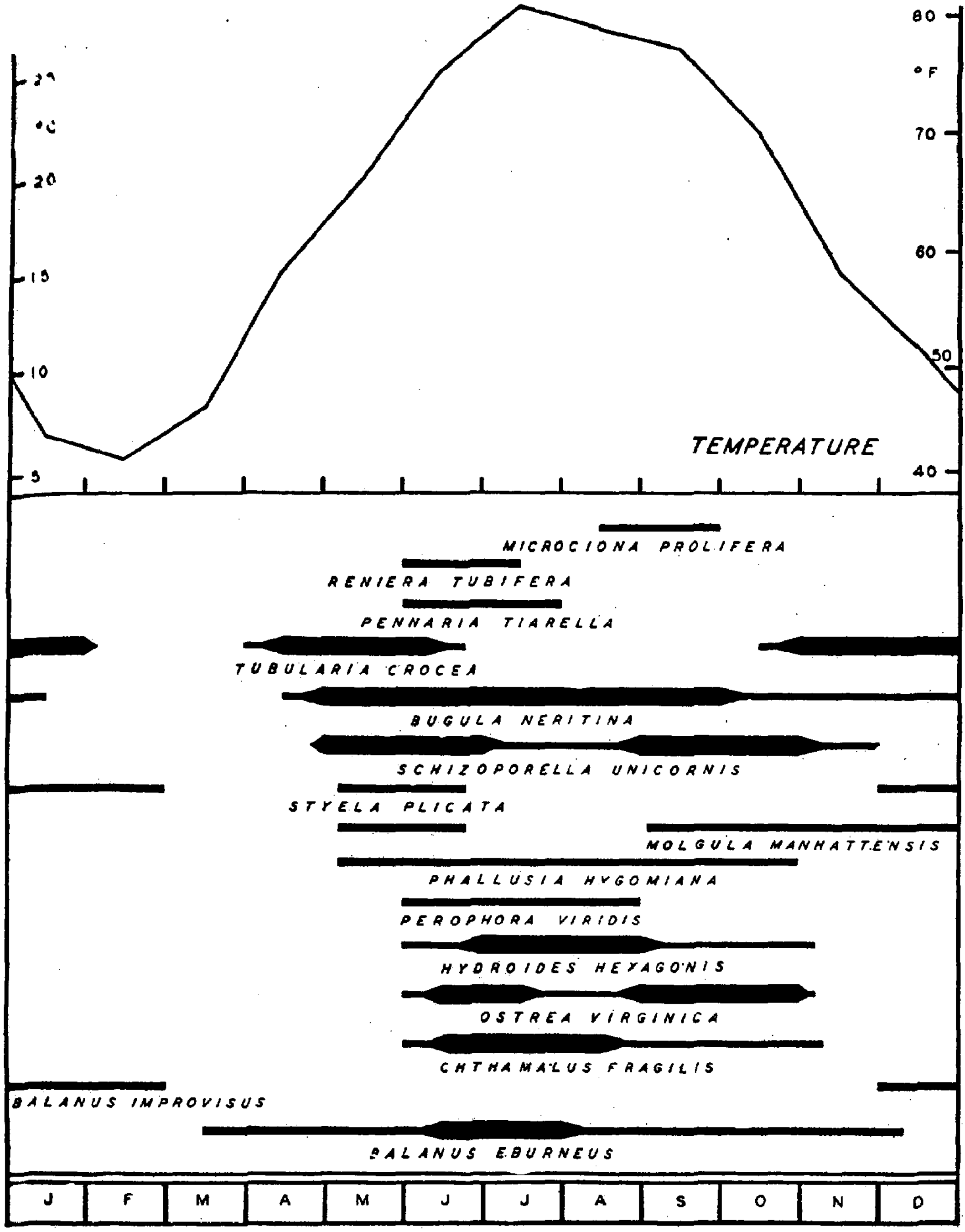
Reproductive periods of some bryozoans at Beaufort, North Carolina, as determined from the piling studies. May, 1954, through April, 1955. Numbers following each species designate the station for each record.

Fig. 9C. Encrusting animals on piling in channels of Beaufort Inlet, N.C. (Maturo, 1959).


13
14
15
16
17
18
19
20
21
22
ROLLOVER
GILCHRIST
ROLLOVER PASS
N
S
SCALE OF MILES
0 1 2 3 4 5

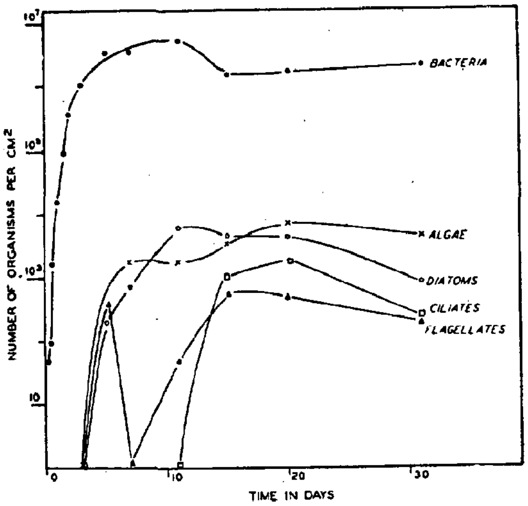
Salinity distribution pattern in East Bay in June, 1956. Isohalines are based on averages at stations occupied.

Fig. 11. Rollover Pass and East Bay (Galveston Bay), Texas (Reid, 1957).



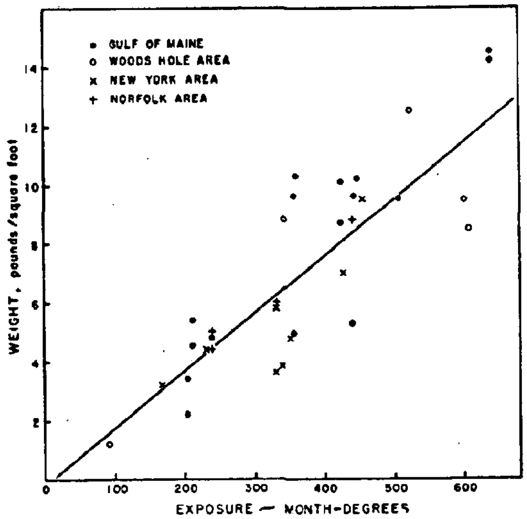
Beaufort, North Carolina. Fouling on wooden and glass surfaces exposed for short and long periods between February 1941 and February 1942, by McDougall (*23*), and on glass panels one month between November 1940 and February 1942, by Ketchum *et al.* (*20*). Temperatures are mean monthly values at Piver's Island, 1914–1928, from McDougall, after Gutsell.

Fig. 10. Seasonal patterns of set of attached animals near Beaufort Inlet, North Carolina (Woods Hole Oceanographic Institution, 1952a).



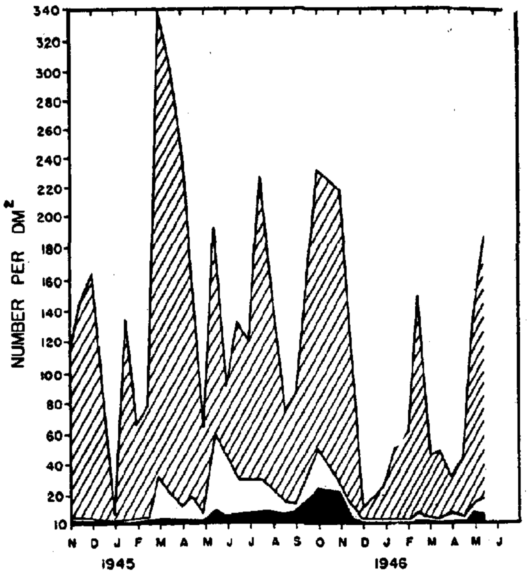
Temporal sequence of bacteria, algae, and protozoa in the slime film developing on a surface immersed in the sea.

Fig. 12. Early succession (Woods Hole Oceanographic Institution, 1952a).



Weight of mussel fouling related to month-degrees of exposure. After Hutchins and Deevey (*12*).

Fig. 13. Growth on surfaces as a function of time and temperature (Woods Hole Oceanographic Institution, 1952a).



Numbers of barnacles attaching to test panels exposed at Miami Beach during successive years. A fresh panel was immersed every 15 days and was examined after one month's exposure. The solid area represents *Balanus eburneus;* the clear area, *Balanus amphitrite;* and the hatched area, *Balanus improvisus*. After Weiss (*42*).

Fig. 14. Seasonal record of new barnacle attachment in Miami Beach waters before modern eutrophication (Woods Hole Oceanographic Institution, 1952a).

Table 2.

Estimated Yearly Accumulation of Mussel Fouling

Location	*Mean Yearly Temperature °F*	*Month-degrees per Year*	*Estimated Fouling lbs./sq.ft./yr.*
Mount Desert Rock	44.7	152	2.72
Boston Lightship	48.3	196	3.55
Fire Island Lightship	52.9	251	4.61
Winter Quarter Lightship	57.5	306	5.65

(Woods Hole Oceanographic Institution, 1952a).

there is light) and associated small animals all in less than two weeks. With timing apparently correlated with availability of food to the new stocks, larval releases provide the "set" to start the attached animals. As shown in Fig. 14 at Miami and Fig. 15 in San Diego where the light regime is not varying so sharply, as in N.C., the regime to support the reef organisms and their reproduction is fairly even as is the set and growth. There is some minimum in winter when the light energy to the food chain is less. Contrast the more southern steady patterns with the sharp season in the northern waters of Maine and elsewhere where reproductive activity seems to be timed with the spring-summer blooms of plankton and runoff from melting snows (Fig. 16). In Fig. 13 the growth is related to product of months and degrees suggesting a role for temperature. However, the temperature is following the light energy input to the food chain with a small lag as heat accumulates, thus keeping pace with the accumulation of energy in the food chain which also lags. The sharp changes of monsoon regimes in India have a substitution of species in the reproduction program, but there is some activity continually (Fig. 17).

Bottoms of Moving Ships

Much studied by the Navy are the fouling communities on the bottoms of ships in spite of the toxic paints applied to prevent the growth. Examples are given in Fig. 18.

STRESS DRAINS

Current Factor

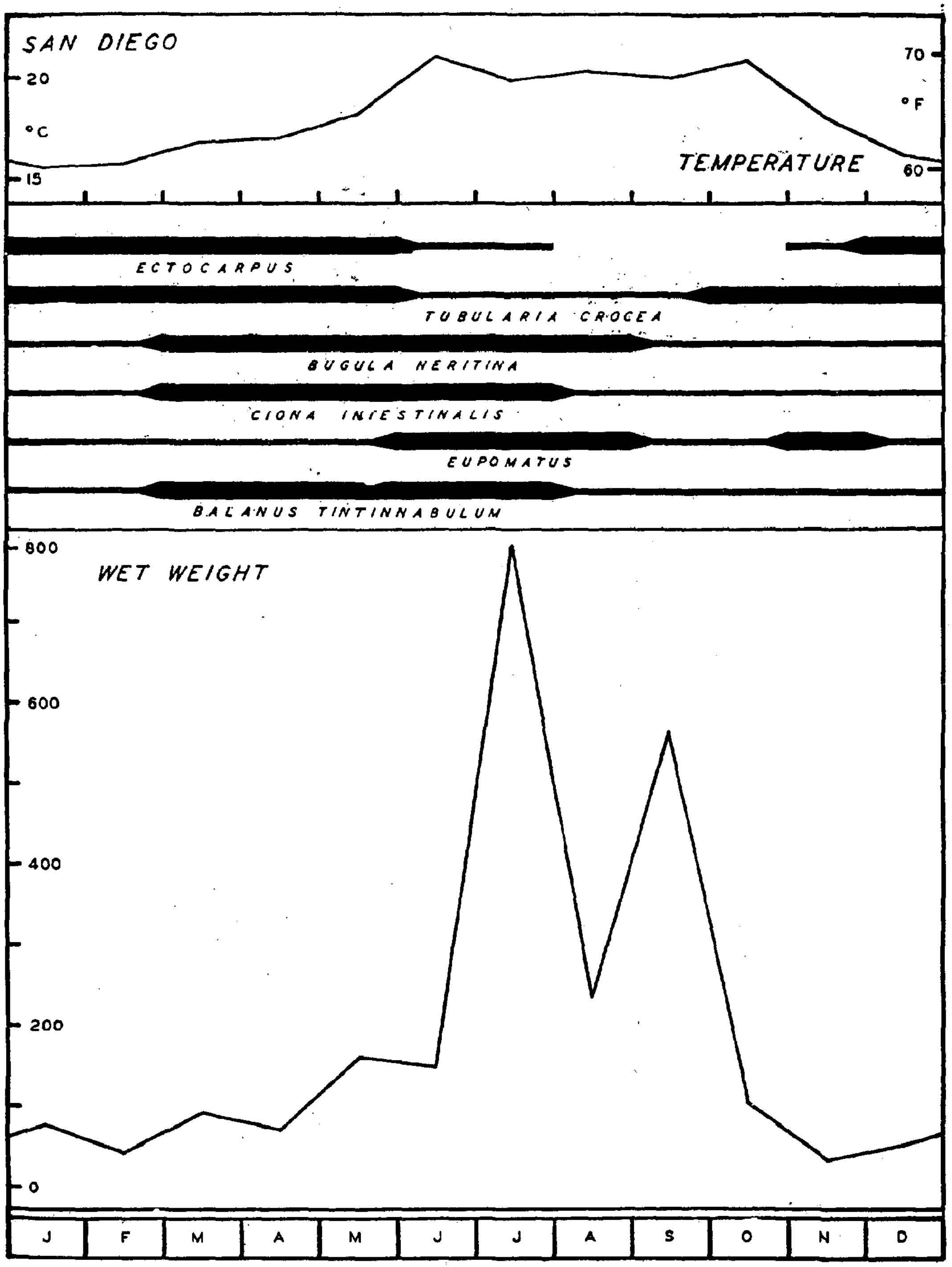
Studies relating the growth of particular fouling species to current show optima as in Figs. 4 and 19. When current is low, the species does not receive enough food and aeration for its internal metabolic setting. When currents are very high the stress of attachment, feeding, and maintenance diminishes the amount of biological structure that can be maintained.

Chemical Stress

Whether chemicals are in the surface material or diffusing in the water, they serve as a stress, require special adaptations, and simplify the variety of the ecosystem which develops and the amount of biotic organization required. The growths on bottoms of ships in spite of anti-fouling paints and harbor pollutants are a good example of the system that results with addition of a man-made chemical stress in addition to the high current stress. An example of copper toxicity diffusing in a gradient so as to limit the high current ecosystem is given in Fig. 18. As stress increases, processes requiring excess energies such as growth and reproduction stop and ultimately there is a concentration at which energy available to the organisms is less than that needed to deal with the stress.

Temperature

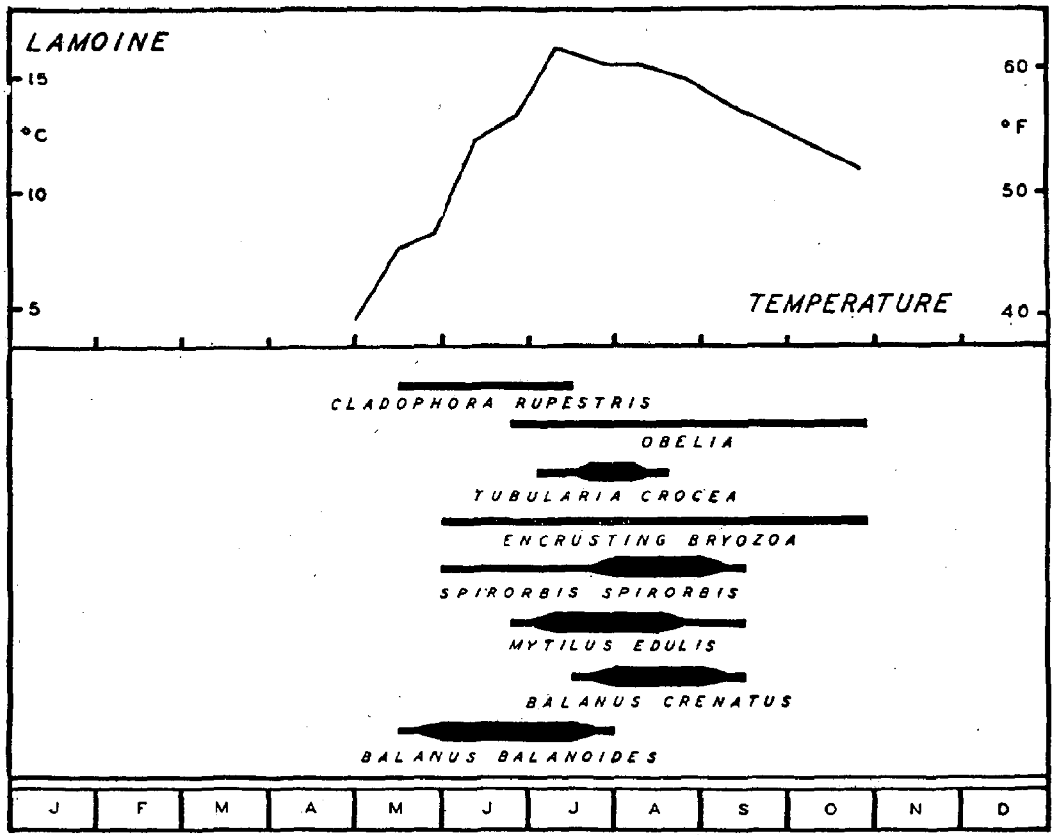
The size of the members of the fouling communities may vary with temperature. It may be that the food niches may be occupied by smaller units of biological machinery at higher temperature because the biochemical processes per



San Diego, California. Fouling of glass and concrete surfaces exposed one month, February 1939 to April 1943. *(Below)* Wet weight of fouling developed per month per square foot of surface. Temperatures: mean monthly values at exposure site 1941–1942. After Whedon (*44*, *45*).

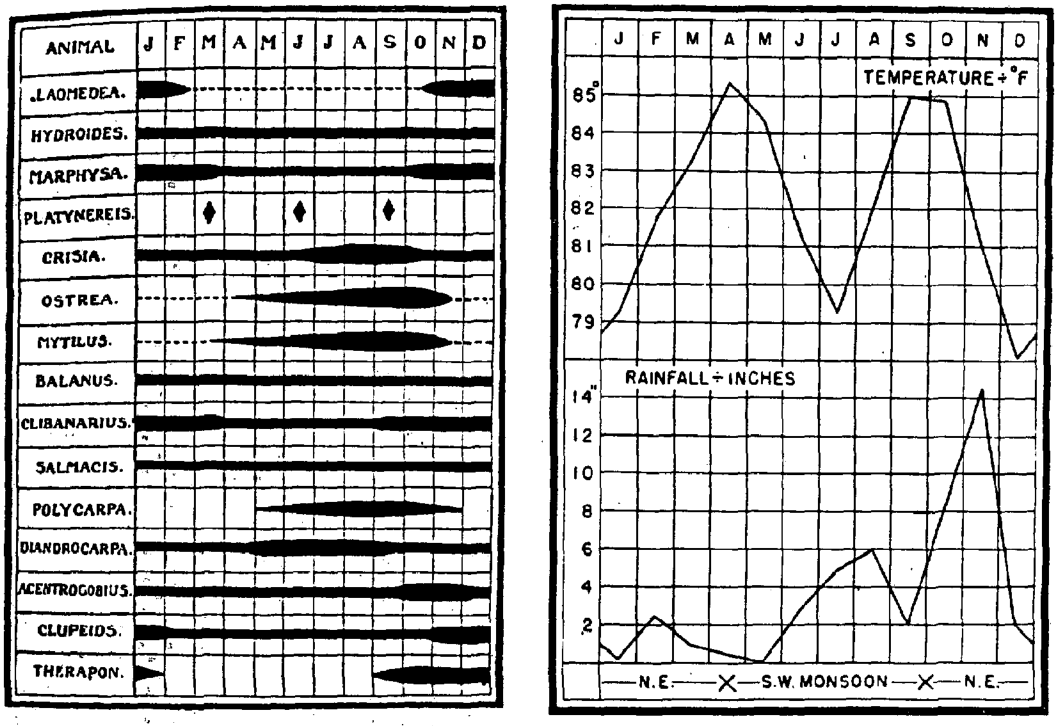
Fig. 15. Seasonal record of larval set and accumulated growth in a subtropical area.

(Woods Hole Oceanographic Institution, 1952a).



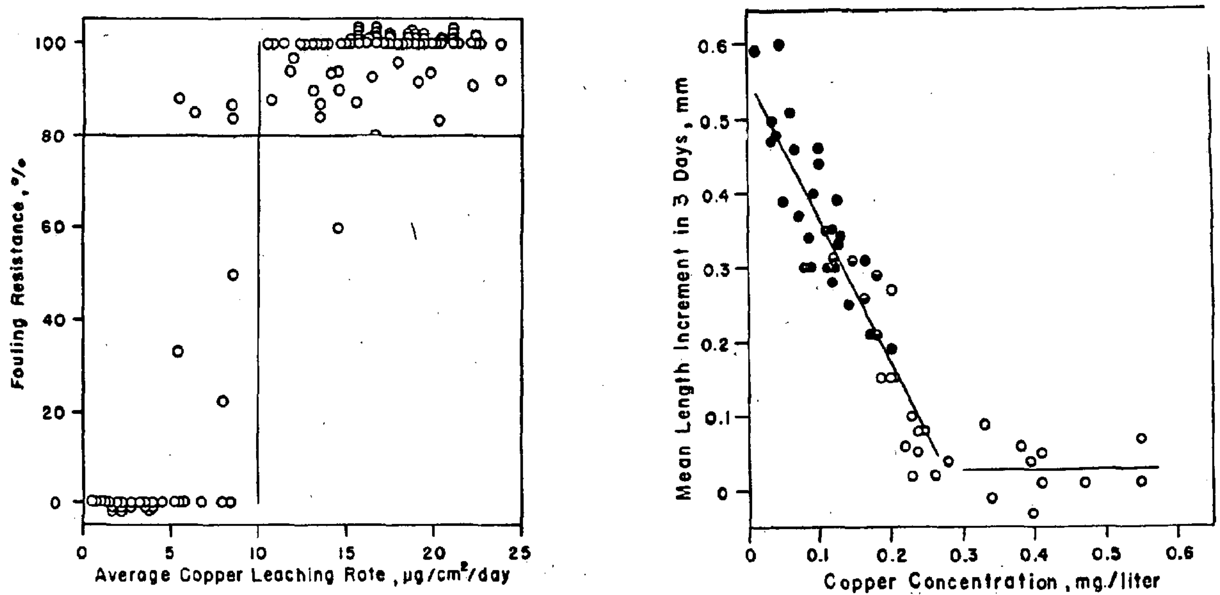
Lamoine, Maine. Fouling on short and long term exposures of collectors, May to October, 1943 and 1944. Temperature as observed at site. After Fuller (*11*).

Fig. 16. Seasonal record of larval set in an Atlantic north temperate location (Woods Hole Oceanographic Institution, 1952 a).



Seasonal variation in temperature of sea water and in rainfall at Madras, India. From data given by Paul. (*Left*) Seasonal variation in breeding of some marine organisms at Madras. After Paul (*32*).

Fig. 17. Seasonal record of larval set in a tropical location with sharp change of Monsoon regimes (Woods Hole Oceanographic Institution, 1952 a).



The average leaching rates, between the second and sixth months of exposure, compared to the fouling resistance, after 6 months, for several different copper antifouling paints. To permit presentation of all of the data some points for 100% fouling resistance are plotted above the 100% line and for 0% fouling resistance below the correct line. These points should be read as 100% or 0% respectively.

Growth of *Bugula* in three days, in relation to copper concentration. ● Fully developed polypides, ◒ partly formed polypides, ○ no differentiation of polypides. Miller (*39*).

Fig. 18. **Graphs of chemical stress (copper) on bryozoan growth (Woods Hole Oceanographic Institution, 1952a).**

Table 3.

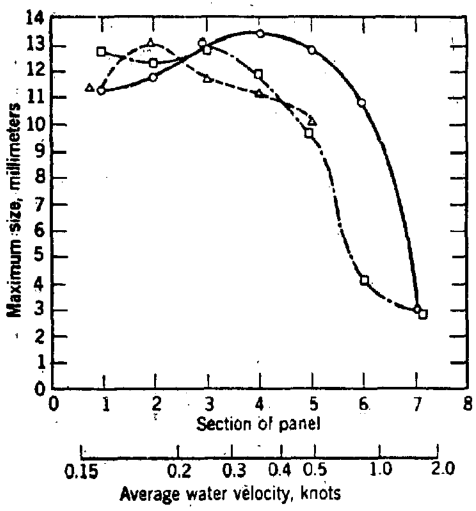
Relation of Rate of Increase of Mussel Fouling to Velocity of Tidal Currents in the Woods Hole Region. Calculations Based on Data of Hutchins and Deevey (*12*)

Name of Buoy	*Mean Current Knots*	*Rate of Increase**
Chatham Lighted Whistle #6	1.02	0.055
Bearse Shoal Lighted Gong #6	1.34	0.047
Old Man Ledge #3	—†	0.044
Pollack Rip Lighted Whistle PR	1.23	0.033
Quicks Hole Bell #1	1.62	0.032
Nantucket Bar Bell	1.02	0.027
Naushon Lighted Bell #20	1.48	0.026
Fifteen Foot Shoal #9	0.95	0.024
Buzzards Bay Lighted Bell #7	0.28	0.019
Gong beside following entry	0.29	0.016
Buzzards Bay Traffic Lighted Buoy #6	0.29	0.014
Block Island Sound Approach Lighted Bell V	0.41	0.013
All Atlantic Coast Buoys—average	—	0.019

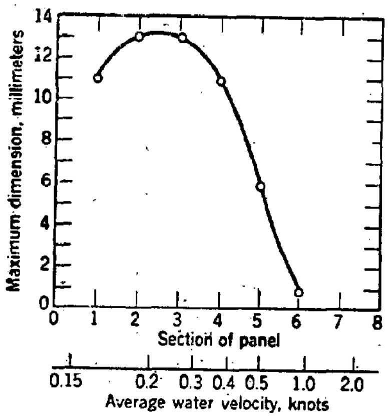
* Rate of increase in pounds per square foot per month-degree.

† Tidal current exceptionally strong in this area. No current data available.

(Woods Hole Oceanographic Institution, 1952a).



The effect of current on the growth of three species of barnacles, *Balanus amphitrite* (circles), *B. improvisus* (squares), *B. eburneus* (triangles). (After Doochin and Smith, 1951.)



Relation of the growth of the bryozoan *Schizoporella unicornis* to water velocity. (After Doochin and Smith, 1951.)

Fig. 19. Graphs of fouling growth as a function of current velocity.

gram may operate faster. Also, at high temperature there is more cost of maintenance program due to thermal degradation that occurs in all structure and must be replaced or repaired.

The high velocity ecosystems are important to man as concentrating mechanisms for food, sports, for waste purification, and as problems in maintaining ships, cooling pipes, and inlets. Those finding the growths as useful yields need to collaborate with those who find them detrimental. Some more general calibration of potential yields as a function of water current may help planning in the future.

The high current system forms as a subsystem in many bays where complexities in current create coarse grained bottoms, shell substrates, epifaunas like small micro-reefs. The associations of high current animals and coarse and shelly bottom substrates in Buzzards Bay, Massachusetts are shown in Figs. 20 and 21.

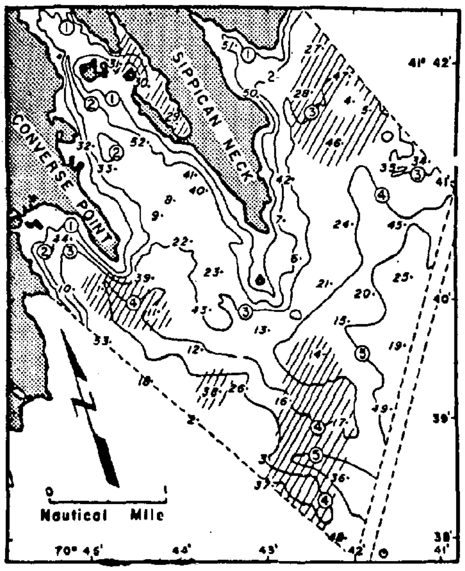

SIPPICAN NECK
CONVERSE POINT
0
1
Nautical Mile
41° 42'
39'
38'
41'
70° 45'
44'
43'
42'

Fig. 20.

Northwest Buzzards Bay. Shaded areas indicate shell-rich substrates. Depth in fathoms are circled, and station numbers are shown in italics

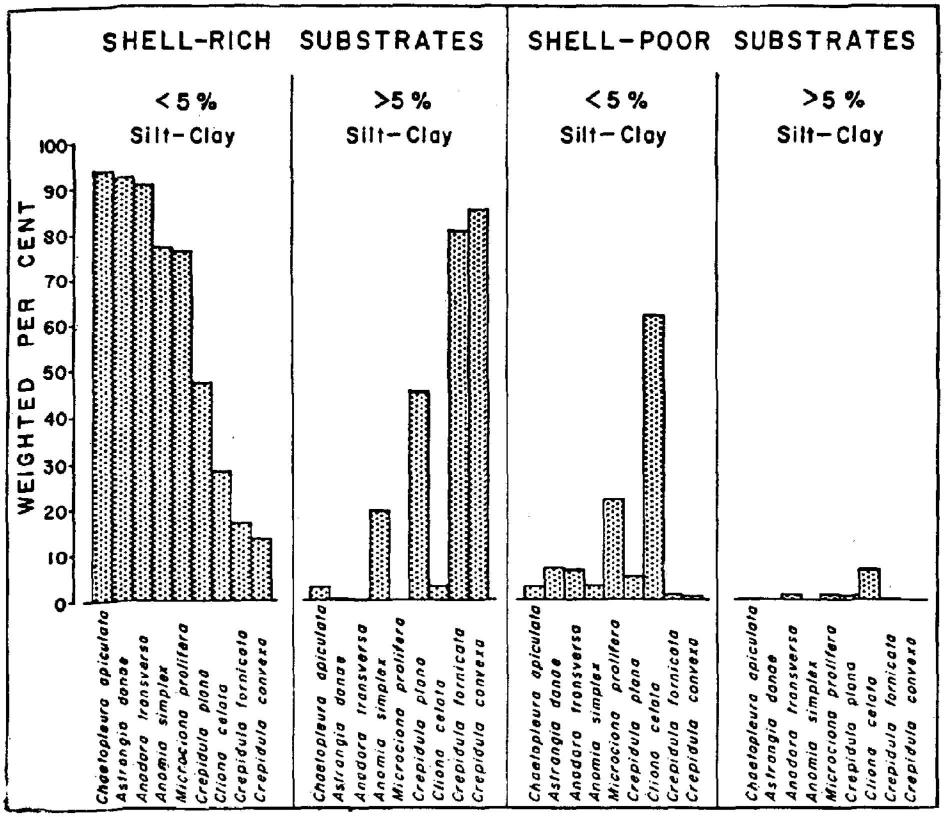


Fig. 21. Bottom animals in Buzzards Bay, Mass. Larger quantities are associated with higher energy environments especially where shell surfaces permit organisms to project above still water of the sea floor (Driscoll, 1967).

Chapter A-4

OSCILLATING TEMPERATURE CHANNELS AND CANALS

In a few places in the United States there are regions bathed with frequently changing waters of wide temperature difference to which few organisms are adapted and in which adapting ecosystems must divert energies from community organization to physiological adaptation. More such situations may develop with more heated water released from power plants and with plans under consideration for navigation channels joining waters of widely differing temperatures. Existing examples of oscillating temperature regime may show the kinds of ecological systems that may adapt.

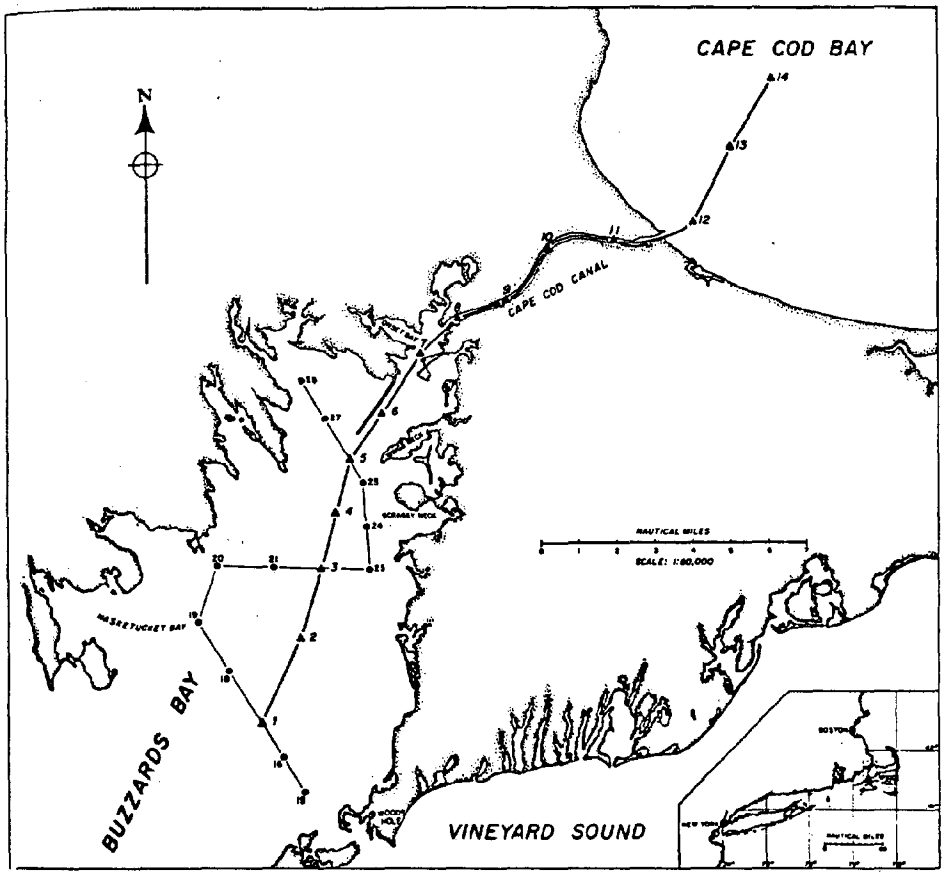
Examples

Cape Cod Canal

As shown in Fig. 1, the Cape Cod Canal at sea level joins colder waters of the Gulf of Maine with warmer marine waters of southern New England. There are several feet of tidal range on the south but a 10 foot range on the north which together pulse waters alternately from the south and from the north through the channel so that temperature ranges may go as high as 27 degrees Fahrenheit. From Anraku (1964a) are shown patterns of salinity (Fig. 2) and distributions of principal zooplankton (Figs. 3, 4, and 5). Chlorophyll data as an index to phytoplankton activity are shown in Table 1. A plankton system is maintained in the canal by the injections of new water. Pseudodiaptomus was more common in the colder waters, Labidocera aestiva in the warmer waters and Acartia tonsa and A. clausii covered the range. Fairbanks, Collings, and Sides (1968) in an abstract describe winter flounder, pollock, cod, tautog, silversides, and herring as principal fishes. Fish eggs in the plankton were of these species and also of cunner, mackeral, rockling and sand lance. Shipworms boring in wood panels increase to the west. Nektonic animals and plankton capable of moving with waters retained some diversity but attached organisms along the shores, stressed by changing temperatures, were low in variety. Frame (1968) found a quasi-steady state of the green algae Ulva, Enteromorpha, and of the tunicate Molgula on the temperature stressed shores. Power plants in the canal may add additional oscillations in temperature. Chlorophyll (Table 1) data show a productive system maintained in the mixing.

New Panama Canals

Very controversial is the proposed sea level Panama Canal which has some properties in common with the Massachusetts sea level canal. South of Panama there are 20-foot tides, variable salinities due to heavy runoff, and


CAPE COD BAY
N
14
13
12
11
10
CAPE COD CANAL
6
5
4
3
2
1
NAUTICAL MILES
SCALE: 1:80,000
WASQUETUCKET BAY
BUZZARDS BAY
VINEYARD SOUND
WOODS HOLE
BOSTON
NEW YORK

Location of standard stations (1–13) occupied on the section Buzzards Bay–Cape Cod Canal–Cape Cod Bay. (Station 14 was occupied only occasionally.) The largest streams, the Weweantic and Wareham rivers, enter to the northwest of Station 28. These presumably account for fresher water between Cape Cod Bay water and Buzzards Bay water.

Fig. 1. Map showing Cape Cod Canal (Anraku 1964a)

TABLE 1 *Mean chlorophyll* a *($\mathrm{mg/m^3}$) in each water mass*

Date	Buzzards Bay water	"Canal" water	Cape Cod Bay water
19 Sept 1960	7.8	4.3	5.5
15 Dec 1960	2.7	2.3	2.4
5 July 1961	2.4	2.9	0.7
14 Aug 1961	2.4	1.3	0.8

(From Anraku 1964a).

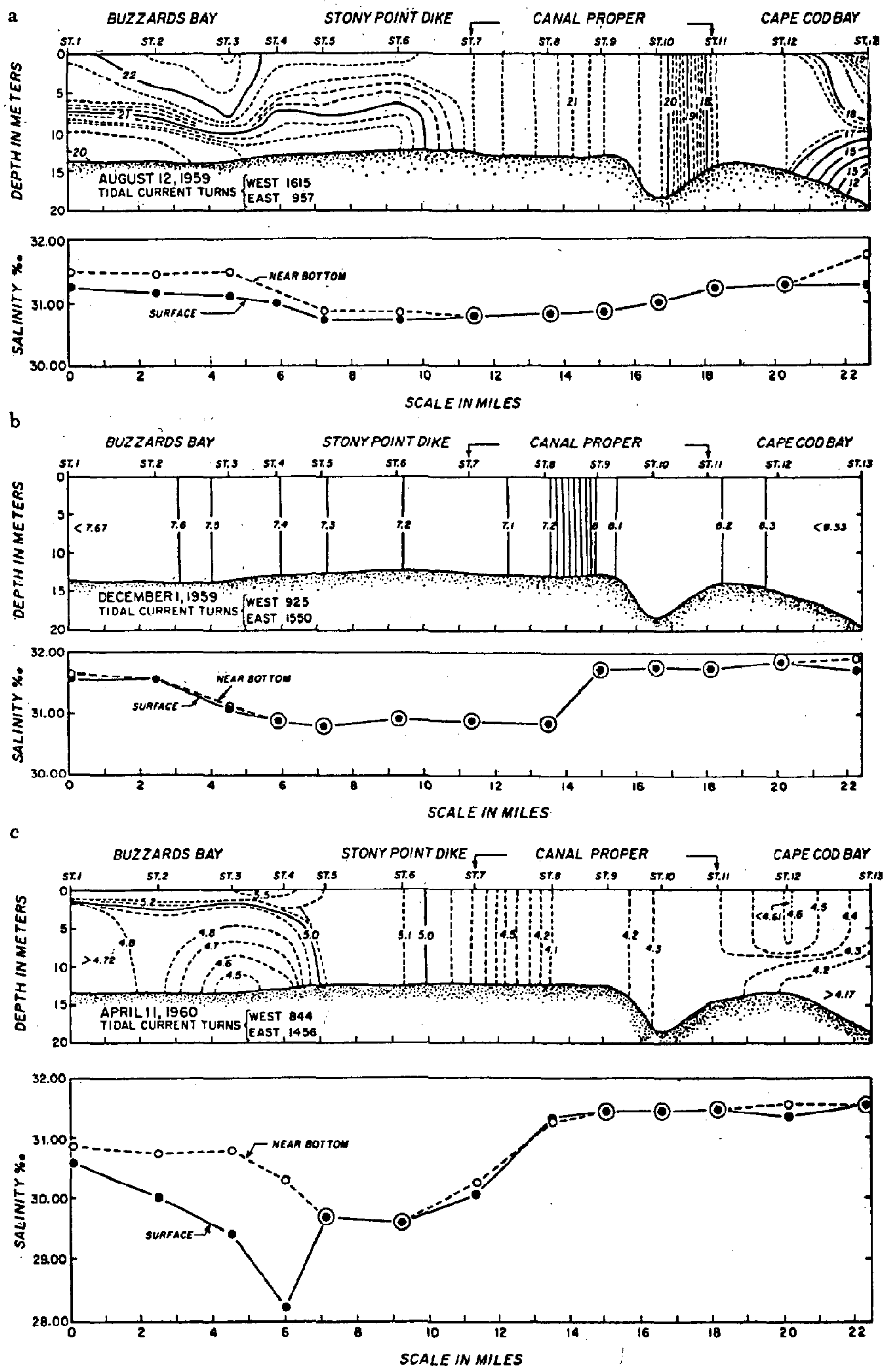
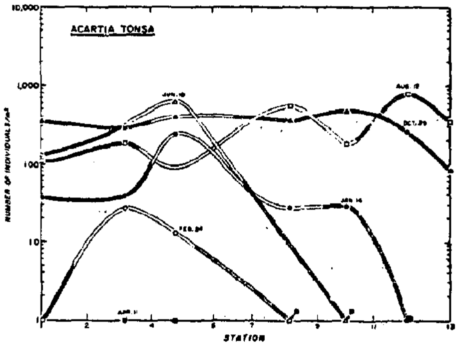
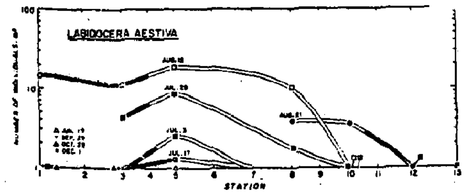


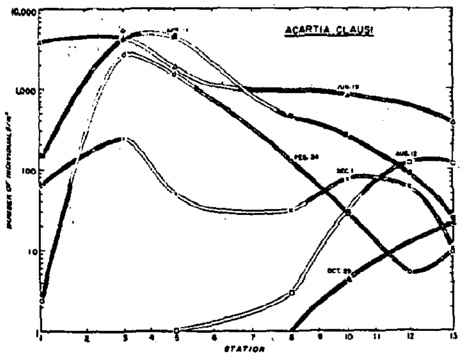
Fig. 2. Salinity patterns in the Cape Cod Canal (Anraku, 1964a).



Distribution of *Acartia tonsa* throughout the year at each station, plotted on logarithmic scale. Figures indicate the number of individuals per m³ taken with a No. 2 net. Ranges of Cape Cod Bay water and Buzzards Bay water are indicated by the stippled and solid line, respectively.



Distribution of *Labidocera aestiva* throughout the year at each station, plotted on logarithmic scale. Figures indicate the number of individuals per m³ taken with a No. 2 net. Ranges of Cape Cod Bay water and Buzzards Bay water are indicated by the stippled and solid line, respectively.



Distribution of *Acartia clausi* throughout the year at each station, plotted on logarithmic scale. Figures indicate the number of individuals per m³ collected with a No. 2 net. Ranges of Cape Cod Bay water and Buzzards Bay water are indicated by the stippled and solid line, respectively.

Figs. 3, 4, and 5. Copepod distribution in the Cape Cod Canal (Anraku, 1964a).

colder waters due to upwelling part of the year. North of the isthmus tides are small and temperatures higher and salinities steady. Diversities are large to the north and small to the south. Discharge of freshwaters into the canal are predicted as large. In this feature the proposed canal resembles the Cross Florida canal which receives much freshwater from porous limestone aquifers so that there is a salinity gradient.

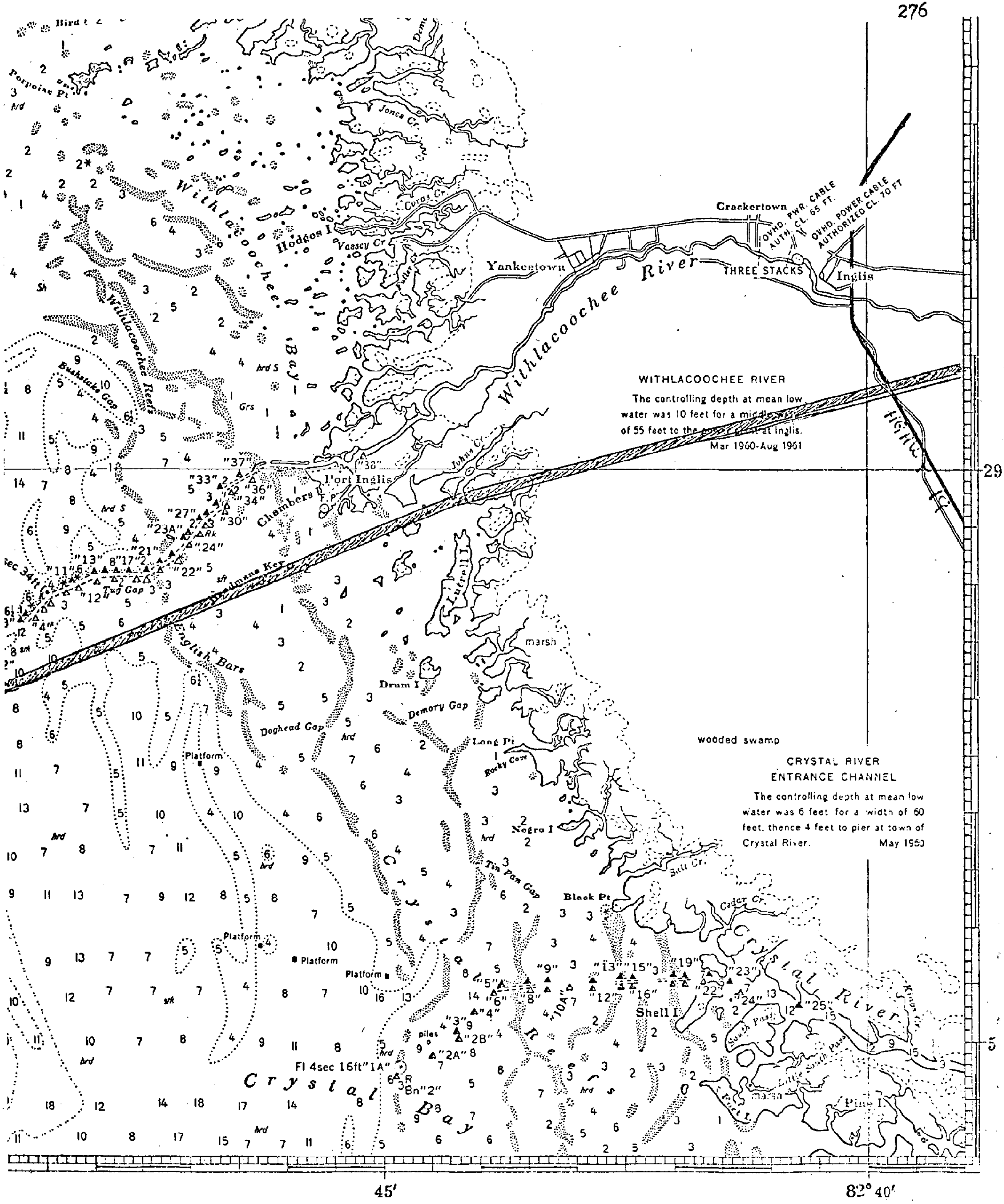
Cross Florida Canal

C. A. Willis, Florida Board of Conservation, supplied the following statement in 1968 about the west end of the new barge canal (Fig. 6) prior to the start of use by barges.

> "The canal itself has provided good trout, redfish, whiting, yellowtail and sheepshead fishing as the fish have sought this deeper water during the winter months. It has provided the only place on this section of the coast where people can fish for salt water fish from the bank.
>
> "It has also produced a very good growth of oysters along the several miles of canal between Highway 19 Bridge and the edge of the Gulf. This is attributed mostly to the proper salinity obtained by the fresh water in the limestone leaching into the salt water flowing up from the Gulf. This short stretch of canal has produced thousands of bushels of oysters--both to the commercial harvester and to the fishing public. The newly exposed limestone rock along the banks has also provided a good cultch for the spat (small oysters) to catch and grow on. It is not uncommon to find a thousand people fishing here on a Saturday or Sunday in the wintertime.
>
> "The seven miles of islands created offshore as spoil banks have also provided a good feeding ground for mullet, big redfish and large trout. The small rocks along the beaches have provided shelter for hundreds of thousands of small crabs -- mostly small stone crabs and oyster crabs. This in turn has attracted and held the fish that feed on them -- blackfish, redfish, sheepshead, etc.
>
> "The islands themselves have provided nesting areas for many of our shore birds. It is easy to walk along the high spots and, if you look very carefully, to find many nests of the Least Tern in the summertime."

Suez Canal

For species to displace others requires that the regimes of stress and ranges of temperature and salinity adaptation be similar. In the Suez Canal in Egypt, the building of the Aswan dam is allowing higher and more regular salinities at the northern end which will allow invasions from



WITHLACOOCHEE RIVER

The controlling depth at mean low water was 10 feet for a middle width of 55 feet to the power plant at Inglis.
Mar 1960-Aug 1961

CRYSTAL RIVER ENTRANCE CHANNEL

The controlling depth at mean low water was 6 feet for a width of 60 feet, thence 4 feet to pier at town of Crystal River. May 1960

Bird I
Porpoise Pt
Withlacoochee Bay
Withlacoochee Reefs
Bushstake Gap
Hodges I
Jones Cr
Coney Cr
Vassey Cr
Crackertown
OVHD. PWR. CABLE AUTH. CL. 65 FT.
OVHD. POWER CABLE AUTHORIZED CL. 70 FT
Yankeetown
Withlacoochee River
THREE STACKS
Inglis
Highway
Port Inglis
Johns Cr
Chambers I
Tug Gap
English Bars
Lutrell I
marsh
Drum I
Demory Gap
Doghead Gap
Long Pt
Rocky Cove
Negro I
Tin Pan Gap
Black Pt
Salt Cr
Cedar Cr
wooded swamp
Crystal River
Shell I
South Pass
Little South Pass
Fort I
Pine I
Platform
Fl 4sec 16ft "1A"
Crystal Bay
29
5
45′
82° 40′

Fig. 6. Western end of the Cross Florida Barge Canal.

the Red Sea not possible before, even though there are some hypersaline conditions in the canal's middle section that reduce viable transport. Thus the Suez example may not be a good model for predicting immigration in Panama. The properties of changing conditions likely to develop in the canal as a continuing stress are likely to result in a simple community, with fewer species than at either end. Odum, Cuzon, Beyers and Allbaugh (1963) found diminished species in Aransas Pass inlet where a similar stress of mixing occurs. Whereas such patterns are probably no barrier to the occasional injection of some species of one area into the zones of the other, the presence of an inhospitable system in between precludes much population pressure. The experience with the Cape Cod Canal shows that mere injection of species that are adapted to one temperature-salinity regime into a sharply different regime serves only as a minor organic food input.

Representative of some opposition opinion is Briggs (1969) who believes there is danger of the canal's changing large areas. This opinion is held by many systematists and evolutionary biologists who regard the historical factor as of controlling importance to the distribution of species.

Chapter A-5

SEDIMENTARY DELTAS

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Columbia, South Carolina

INTRODUCTION

Deltas (Fig. 1-4) are massive accumulations of sediment built up where rivers enter a lake, an enclosed sea, bay, or lagoon, or the open ocean. Where deltas occur it is an indication that sediment is being supplied by the river at a more rapid rate than it can be removed by tidal currents, wave action, and other forces in the basin of deposition. Thus the most significant stress, from the ecological viewpoint, is the high sedimentation rate that characterizes the environment associated with deltas. Whether or not a river develops a delta is affected not only by its sediment load but by its discharge as well. Rivers that discharge less than 500 cubic feet/second are unable to counterbalance wave action. Those with discharges around 15,000 cubic feet/second develop cuspate deltas without distributary channels. Discharges upwards of 50,000 cubic feet/second are needed to initiate and maintain the large distributary systems that characterize the world's major deltas and to extend them quickly enough to overwhelm marine erosion. A characteristic ecological system develops in the waters and on the bottom in the zones of river discharge into the sea.

EXAMPLES

Mississippi River

Within the United States the best known and largest example is the Mississippi delta that dominates the state of Louisiana. In addition to the ecosystem at the mouths of the distributaries, there are other ecological systems and subsystems such as the oyster reefs, marshes, and oigohaline bays, covered in other chapters. Maps and diagrams showing the Mississippi delta, some sedimentary characteristics, and some of the biological components and processes are given in Figs. 5-18. Zones and sediments are in Figs 5 and 6. Salinity in relation to current is given in Figs. 7 and 13, temperature in Fig. 8. Changes in temperature profiles after hurricane passage are given by Stevenson (1966) in Fig. 16. The relatively restricted variety of organisms are summarized in Table 1 by Parker (1960) Foraminifera are summarized by Walton (1964) in Fig. 14 and Curtis (1960) in Fig. 15. Ratios of sand, silt, and clay are given in Figs 17 and 18.

Añasco River, Western Puerto Rico

The delta of a very small tropical river in western Puerto Rico is of special interest because of the trace element studies and the environment of blue tropical waters and coral reefs. The Añasco River and some properties of sediments are given in Figs 19-30 (Lowman 1966, Lowman et al. 1966, Lowman et al. 1967).

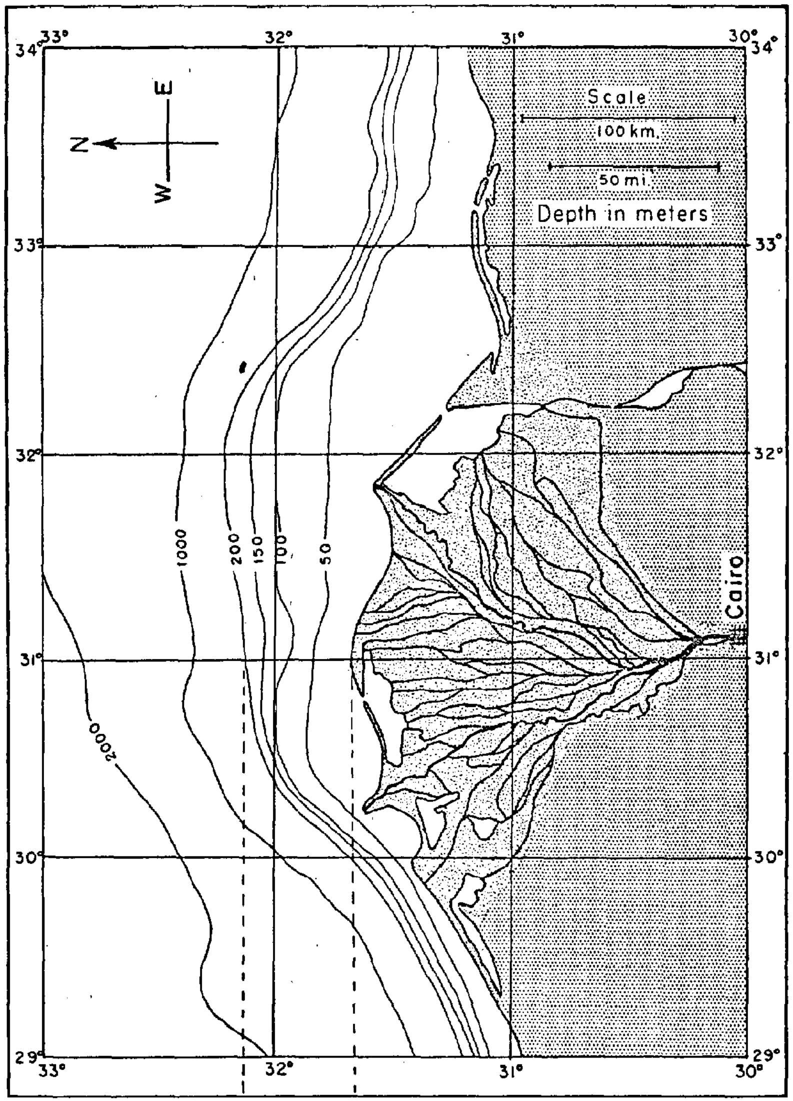

33°
32°
31°
30°
34°
E
N
W
Scale
100 km.
50 mi.
Depth in meters
33°
32°
31°
30°
1000
200
150
100
50
2000
Cairo
29°
33°
32°
31°
30°

Figure 1A

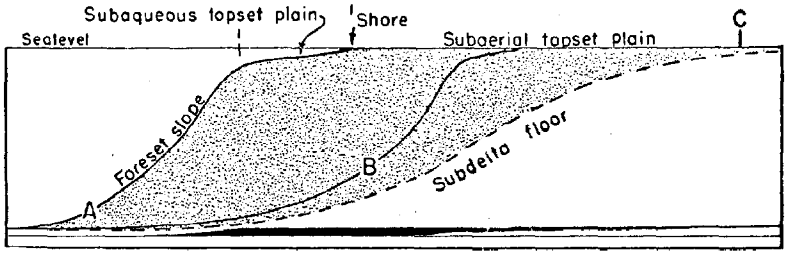
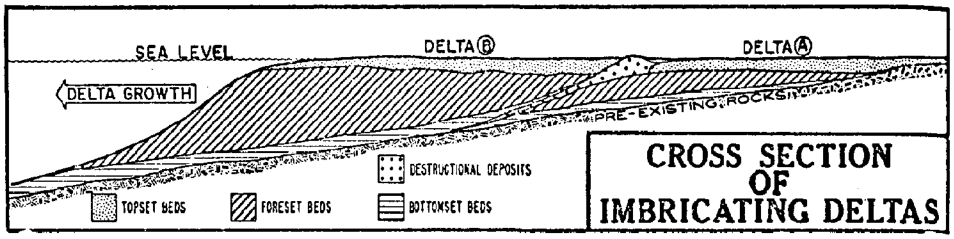

Subaqueous topset plain
Shore
C
Sealevel
Subaerial topset plain
Foreset slope
A
B
Subdelta floor

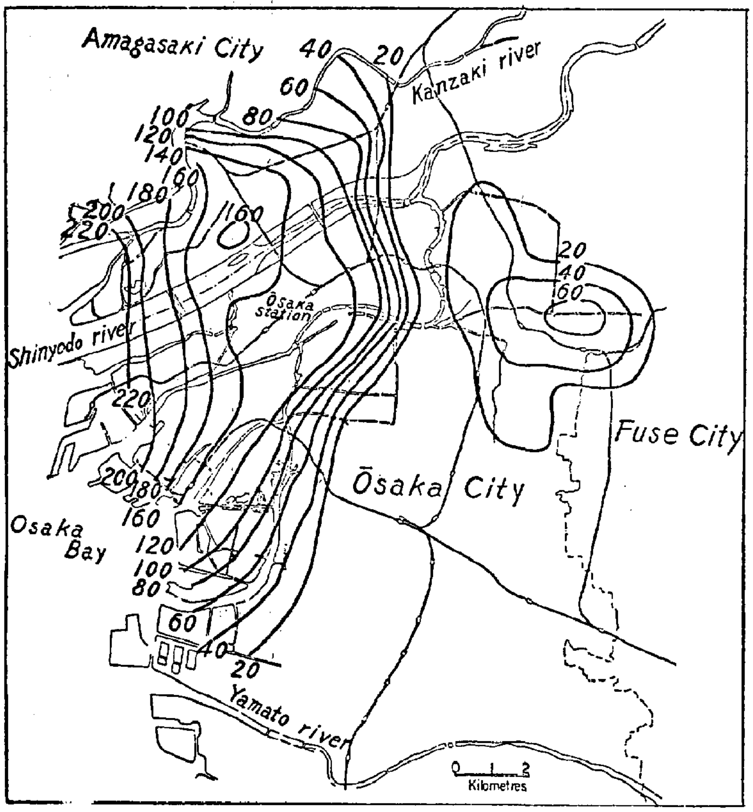
Figure 1B

The Nile Delta. Map: subaerial part of delta shown by darker shading, subaqueous part by subm (depths in meters). Cross sections: profile A along 31st meridian in center of delta—shading shows probable thic sediment (upper section exaggerated about 80 times; lower section nearly true scale); profile B along 29th me delta.


SEA LEVEL
DELTA B
DELTA A
DELTA GROWTH
PRE-EXISTING ROCKS
DESTRUCTIONAL DEPOSITS
TOPSET BEDS
FORESET BEDS
BOTTOMSET BEDS
CROSS SECTION OF IMBRICATING DELTAS

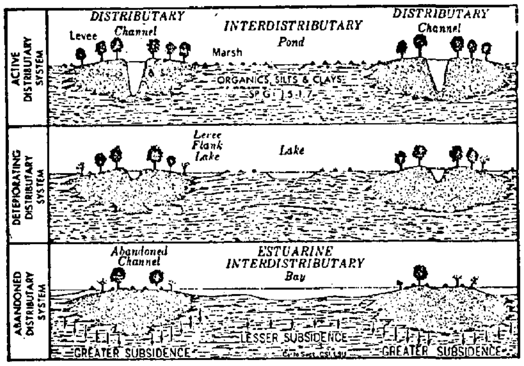
—Shows schematically the vertical relations between constructional and destructional deposits in imbricating deltas. Stratigraphic units of successive deltas merge, and may appear correlative over wide areas. Thicknesses of individual deltas depend on depths of water when deposition begins.

Figure 2


Amagasaki City
Kanzaki river
Shinyodo river
Ōsaka Station
Fuse City
Ōsaka City
Osaka Bay
Yamato river
20
40
60
80
100
120
140
160
180
200
220
0 1 2
Kilometres

EQUAL LINES OF LAND SUBSIDENCE IN OSAKA CITY, FROM 1935 TO 1960. (IN CENTIMETERS)

Figure 3


ACTIVE DISTRIBUTARY SYSTEM
DETERIORATING DISTRIBUTARY SYSTEM
ABANDONED DISTRIBUTARY SYSTEM
DISTRIBUTARY Channel
Levee
INTERDISTRIBUTARY Pond
Marsh
ORGANICS, SILTS & CLAYS
Levee Flank Lake
Lake
Abandoned Channel
ESTUARINE INTERDISTRIBUTARY Bay
GREATER SUBSIDENCE
LESSER SUBSIDENCE

Effects of deltaic subsidence during distributary system abandonment.

Figure 4

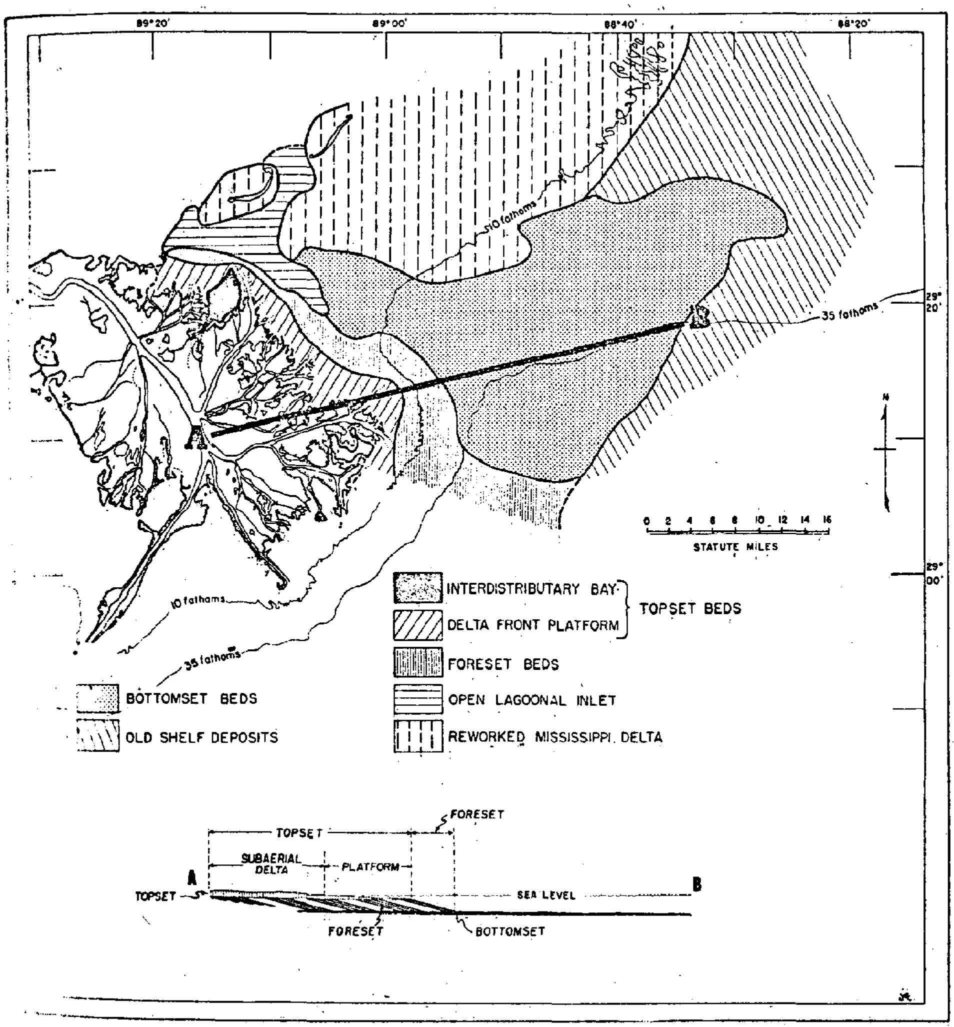

89°20'
89°00'
88°40'
88°20'
10 fathoms
35 fathoms
29° 20'
29° 00'
N
0 2 4 6 8 10 12 14 16
STATUTE MILES
INTERDISTRIBUTARY BAY
DELTA FRONT PLATFORM
TOPSET BEDS
FORESET BEDS
OPEN LAGOONAL INLET
REWORKED MISSISSIPPI DELTA
BOTTOMSET BEDS
OLD SHELF DEPOSITS
TOPSET
FORESET
SUBAERIAL DELTA
PLATFORM
A
B
SEA LEVEL
FORESET
BOTTOMSET

Figure 5

–Sediment environments to the east of lower Mississippi Delta. Relation of these environments [illegible]-set, fore-set, and bottom-set beds is indicated by comparison with the inset at the lower part of [illegible] The slope of the fore-set beds is greatly exaggerated, actually does not exceed 1 per cent. From [illegible] 1958, Fig. 9.

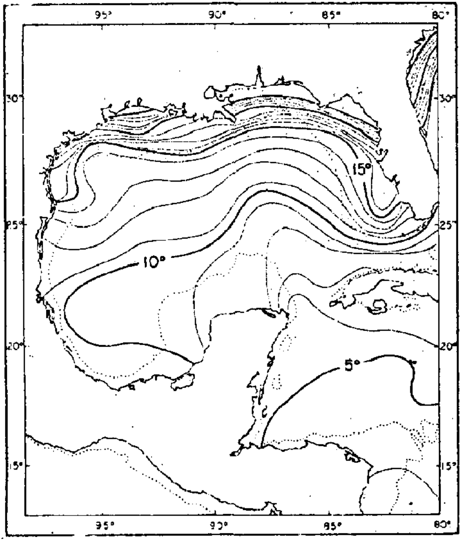
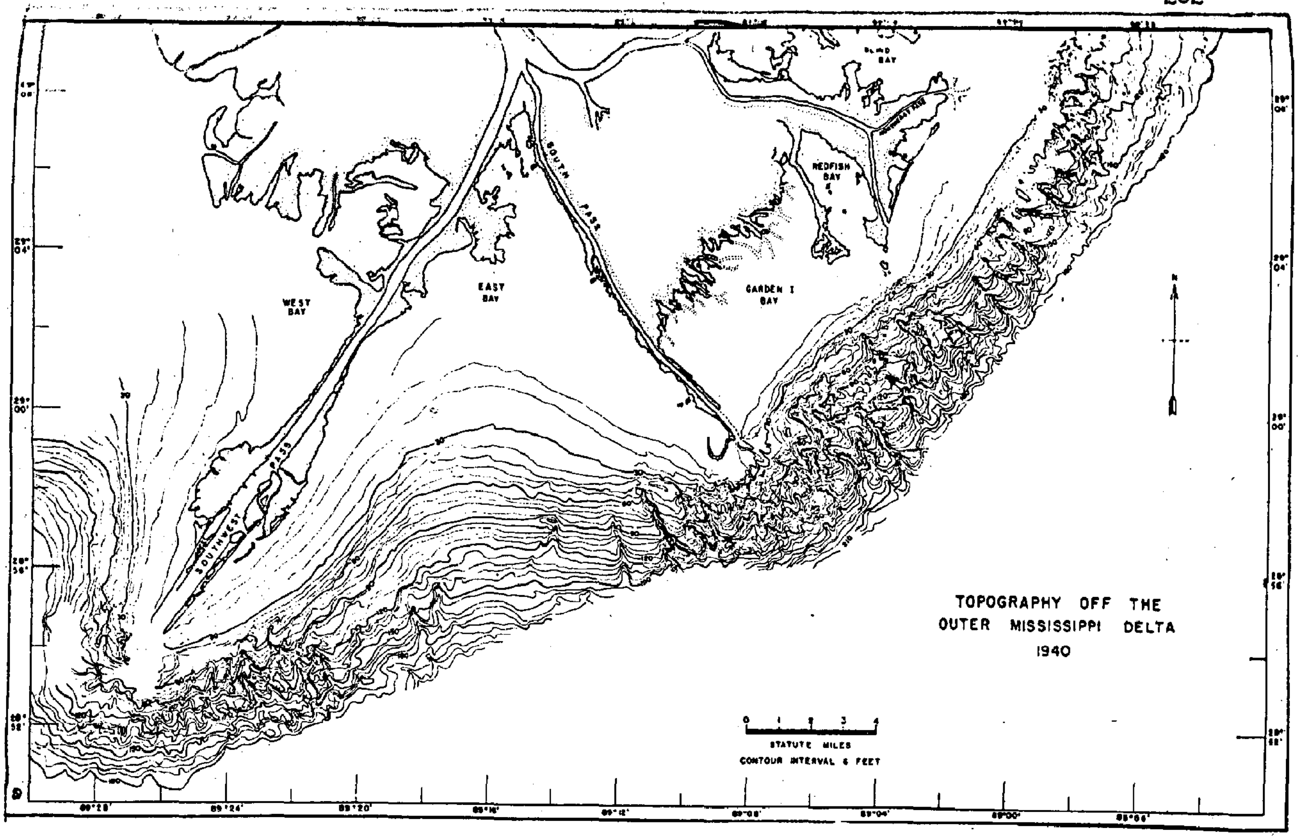

95°
90°
85°
80°
30°
25°
20°
15°
15°
10°
5°

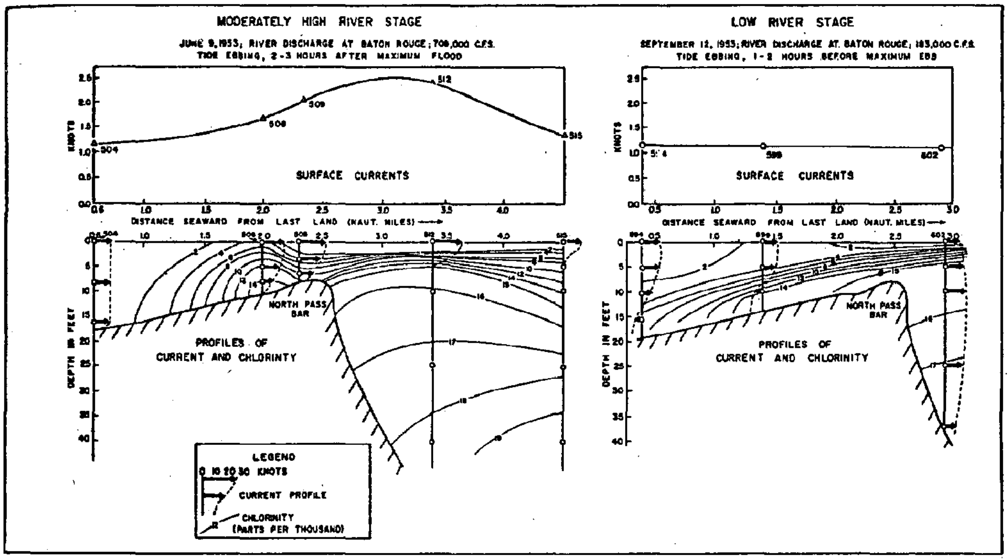
Figure 8

—Difference in surface temperatures in °F between warmest and coldest months. After Fuglister, 1947.


WEST BAY
EAST BAY
SOUTH PASS
SOUTHWEST PASS
REDFISH BAY
GARDEN I BAY
TOPOGRAPHY OFF THE OUTER MISSISSIPPI DELTA 1940
0 1 2 3 4
STATUTE MILES
CONTOUR INTERVAL 6 FEET
89°28'
89°24'
89°20'
89°16'
89°12'
89°08'
89°04'
89°00'
88°56'
29°04'
29°00'
28°56'

–Submarine gullies which are concentrated off the most advanced passes of the Mississippi Delta. From Shepard, 1955, Pl. 1.

Figure 6



Profile showing current velocity and chlorinity at the mouth of North Pass, Mississippi River Delta. Upper diagrams show surface speeds along channel axis. Diagrams on the left show the outward flow during moderately high river stage extending to the bottom at the bar. Salt water included during the preceding high tide is rapidly flushed out during the ebb. Profiles at right show the lower river stage: the current is not affected by the bar, the water rides over the salt wedge, and the speed decreases smoothly in the channel and over the bar (From Scruton, 1960; Shepard, 1960).

Figure 7

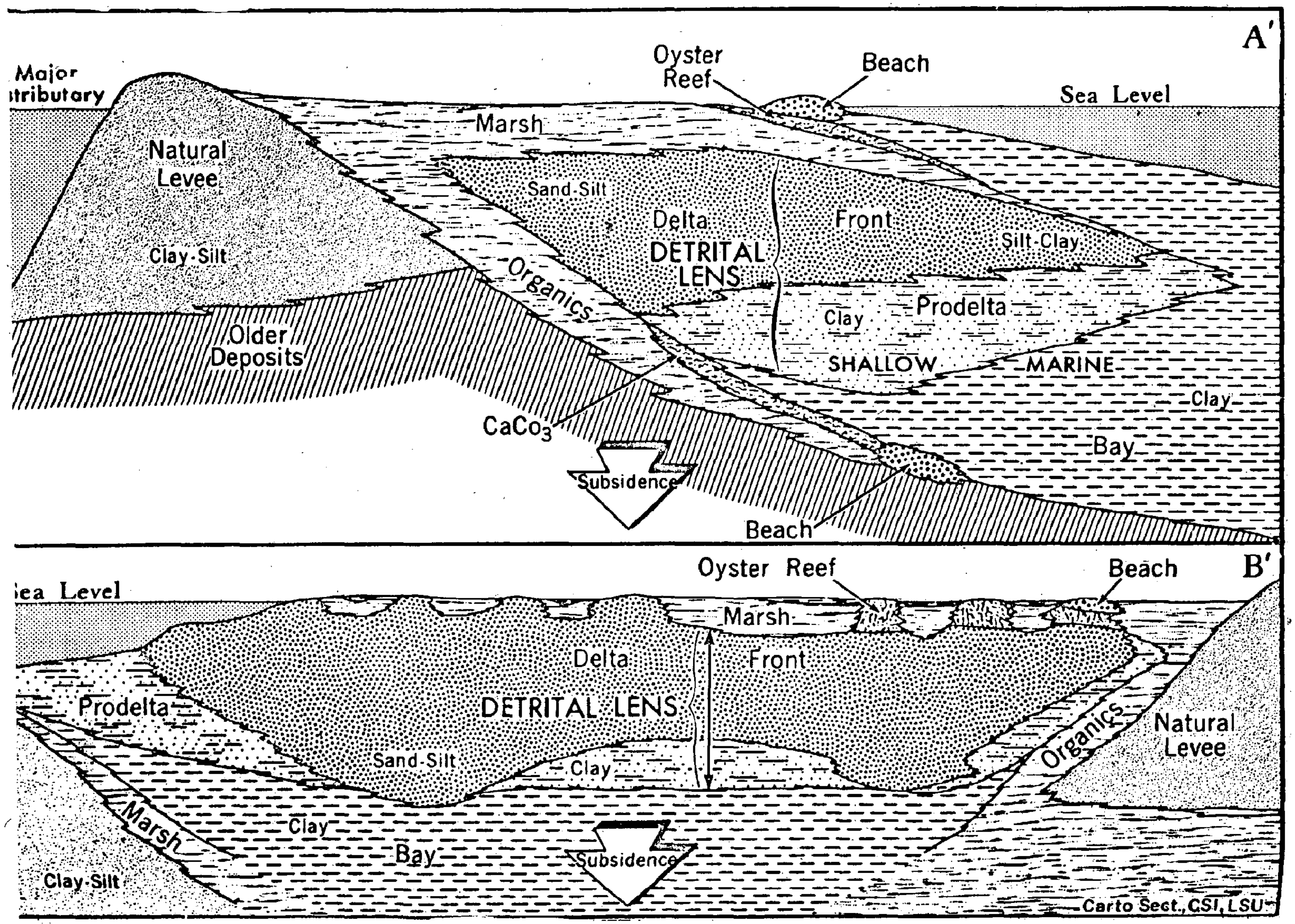

A′
Major
tributary
Oyster
Reef
Beach
Sea Level
Marsh
Natural
Levee
Sand-Silt
Delta
DETRITAL
LENS
Front
Silt-Clay
Clay-Silt
Organics
Clay
Prodelta
Older
Deposits
SHALLOW
MARINE
Clay
CaCo3
Bay
Subsidence
Beach
B′
Oyster Reef
Beach
ea Level
Marsh
Delta
Front
Prodelta
DETRITAL LENS
Natural
Levee
Organics
Sand-Silt
Clay
Clay
Marsh
Bay
Subsidence
Clay-Silt
Carto Sect., CSI, LSU

Fig. 9. Cross section of hypothetical model of delta complex (From Coleman and Gagliano 1964).

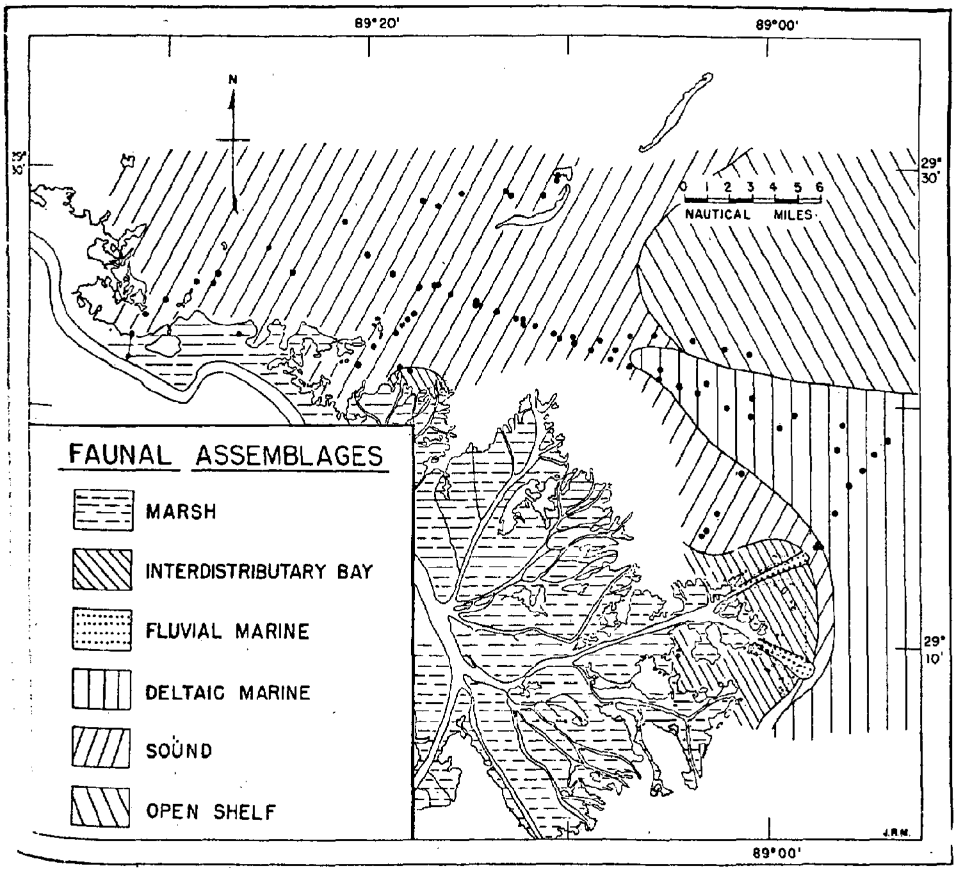

89°20'
89°00'
N
29° 30'
29° 10'
0 1 2 3 4 5 6
NAUTICAL MILES
FAUNAL ASSEMBLAGES
MARSH
INTERDISTRIBUTARY BAY
FLUVIAL MARINE
DELTAIC MARINE
SOUND
OPEN SHELF
J.R.M.

Figure 10

Foraminiferal facies, southeast Mississippi Delta. Black dots are station locations. After Lankford, 1959.

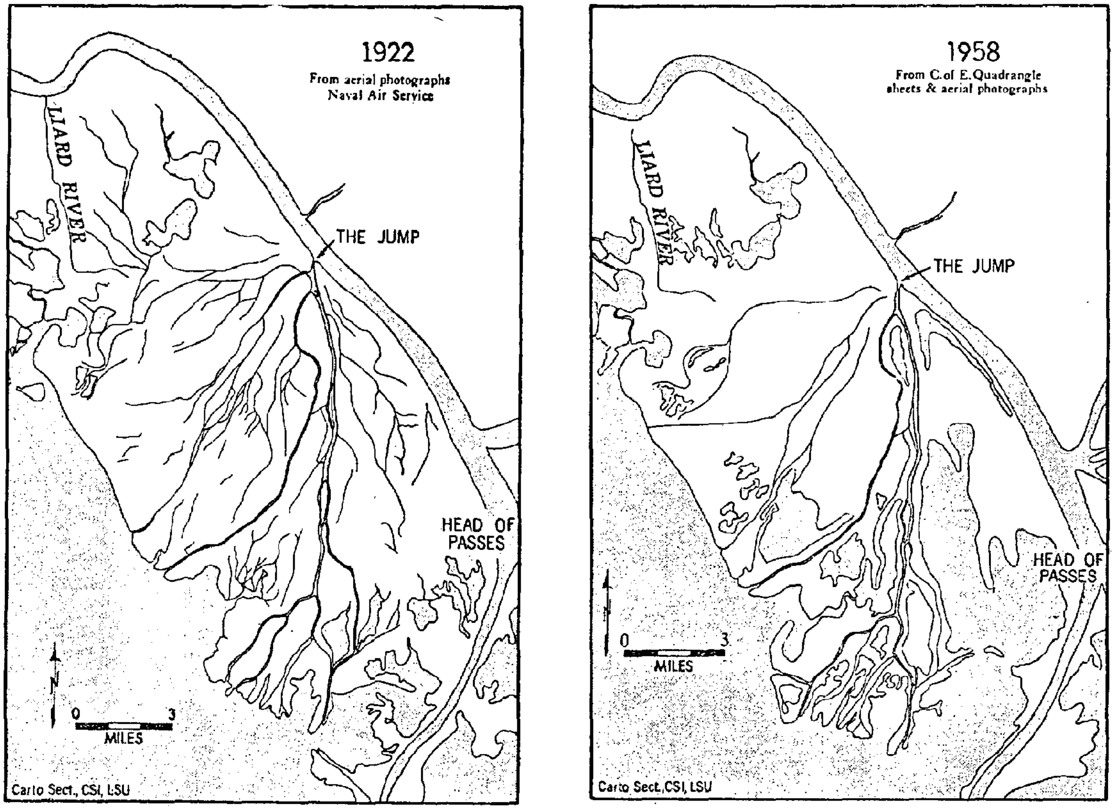

1922
From aerial photographs
Naval Air Service
LIARD RIVER
THE JUMP
HEAD OF PASSES
N
0 3
MILES
Carto Sect., CSI, LSU
1958
From C. of E. Quadrangle sheets & aerial photographs
LIARD RIVER
THE JUMP
HEAD OF PASSES
0 3
MILES
Carto Sect., CSI, LSU

Figure 11

The Jump (West Bay) subdelta near height of depositional activity.

The Jump (West Bay) subdelta showing subsidence effects during present process of abandonment.

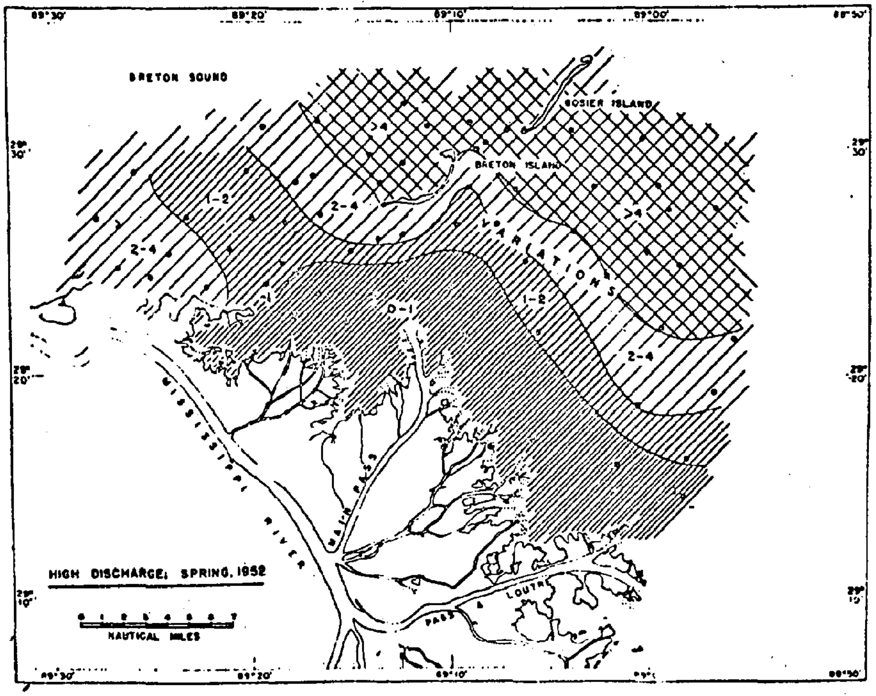

89°30'
89°20'
89°10'
89°00'
88°50'
29°30'
29°20'
29°10'
BRETON SOUND
GOSIER ISLAND
BRETON ISLAND
>4
1-2
2-4
0-1
VARIATIONS
MISSISSIPPI RIVER
MAIN PASS
PASS A LOUTRE
HIGH DISCHARGE; SPRING, 1952
NAUTICAL MILES

Figure 12

·Distribution of suspended matter in surface waters of inshore area, from secchi disc observations. Compare with distribution of surface chlorinity

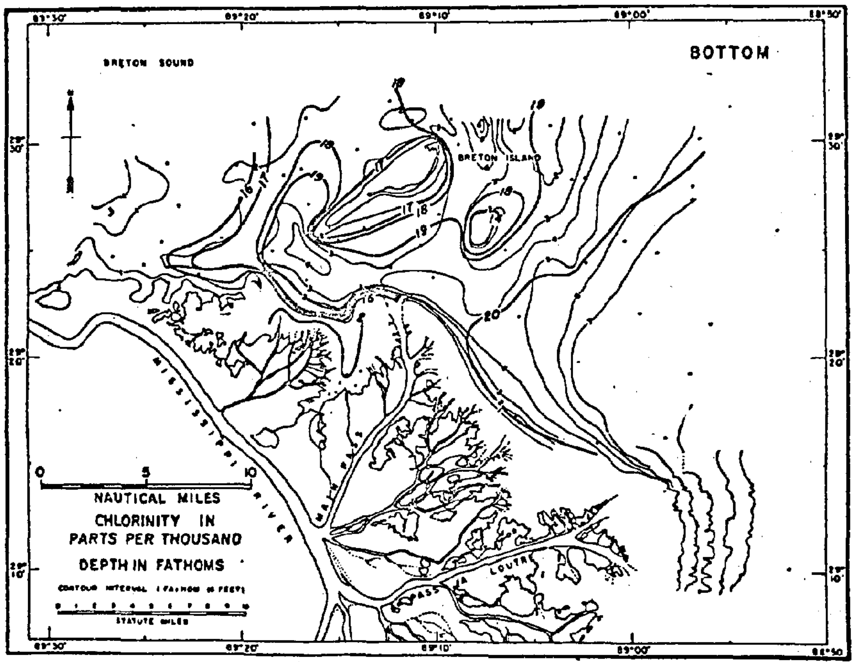
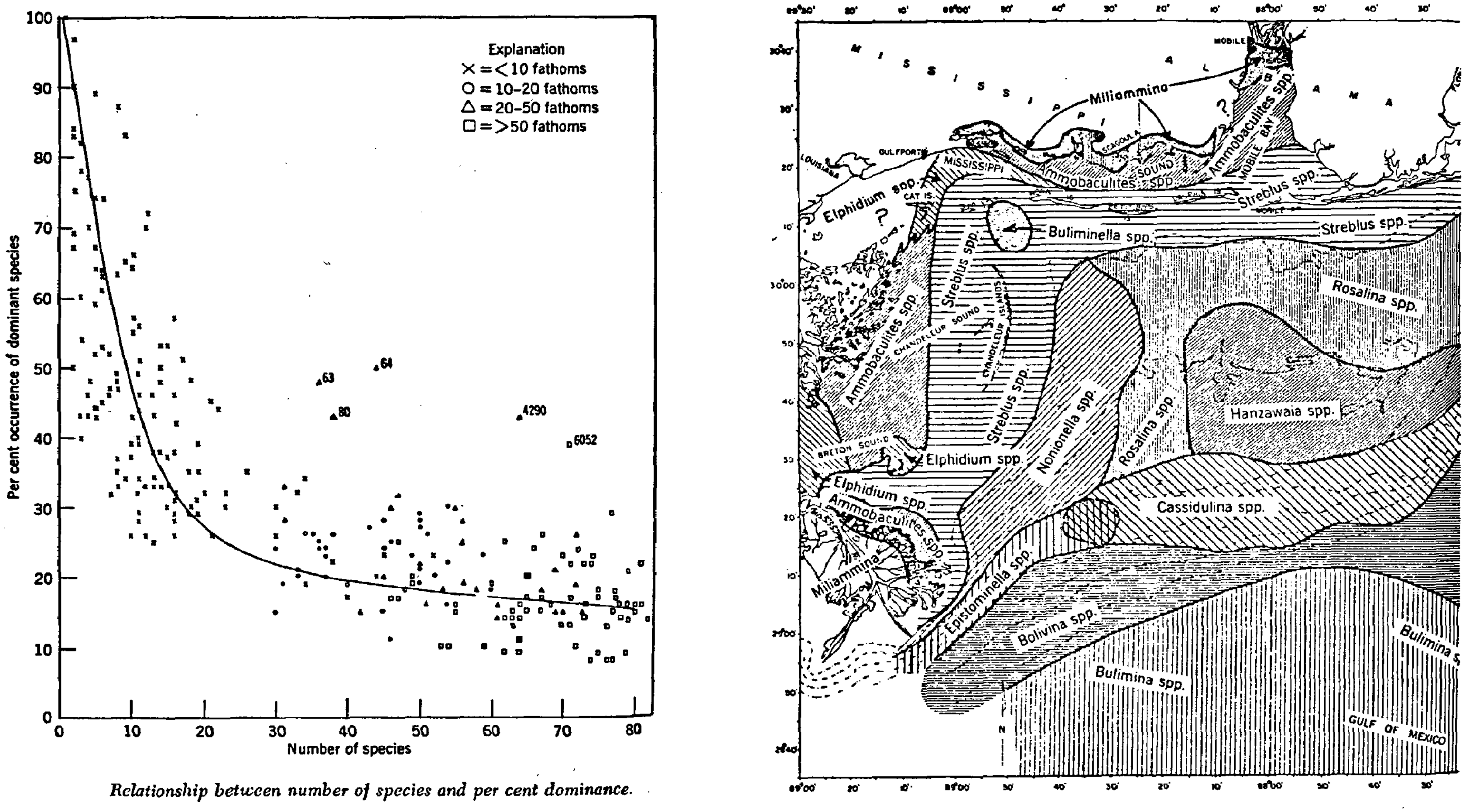

89°30'
89°20'
89°10'
89°00'
88°50'
29°30'
29°20'
29°10'
BRETON SOUND
BOTTOM
BRETON ISLAND
19
18
17
16
20
14
MISSISSIPPI RIVER
MAIN PASS
PASS A LOUTRE
0
5
10
NAUTICAL MILES
CHLORINITY IN PARTS PER THOUSAND
DEPTH IN FATHOMS
CONTOUR INTERVAL 1 FATHOM (6 FEET)
STATUTE MILES

Figure 13

—Inshore chlorinity distribution, spring, 1952, high river discharge, low winds. Bottom chart is maximum observed chlorinities, usually occurring here on flood tide. Surface chart is composite of minimum observed chlorinities. These usually occur on flood tide in Breton Sound and ebb tide east of Main Pass. Chlorinity changes are most pronounced in areas marked "variations" and changes were toward higher chlorinities. These charts show maximum observed vertical chlorinity differences.



Relationship between number of species and per cent dominance.

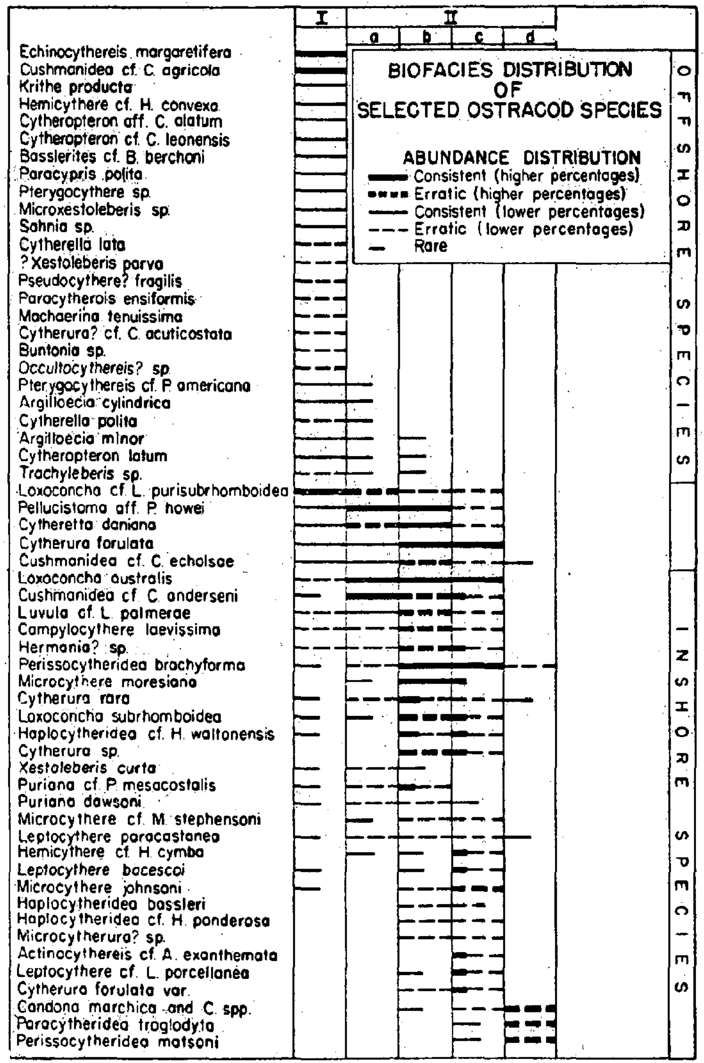
Distribution

Fig. 14. Distribution of foraminifera off the Missisippi River Delta (Walton, 1964).

Table 1. Missisipi Delta animals (Parker, 1960).

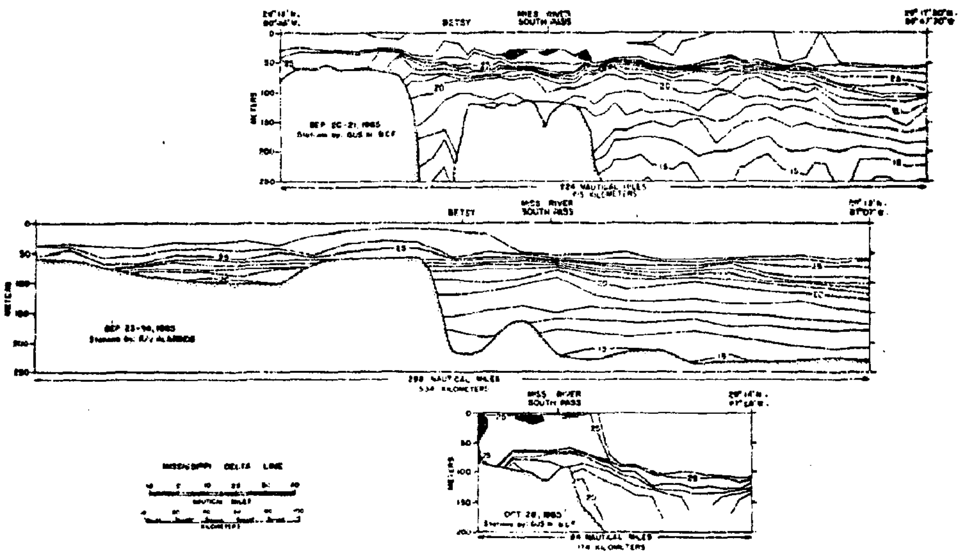
III. DELTA-FRONT DISTRIBUTARY AND INTERDISTRIBUTARY ASSEMBLAGE

Species	*Comparative Abundance; Size*
PELECYPODS	
Rangia cuneata (Gray, 1831)	Not as abundant as in river-influenced assemblage
Rangia flexuosa (Conrad, 1840)	More abundant, especially in interdistributary bays
Macoma mitchelli Dall, 1895	Rare, mostly in channels
Crassostrea virginica (Gmelin, 1791)	Very abundant in higher salinity interdistributary bays; large (2–6 in.)
Petricola pholadiformis Lamarck, 1818	Common on distributary submerged levees; medium (1½–2½ in.)
GASTROPODS	
Littoridina or *Amnicola*, species	Not very common; small (1/16 in.)

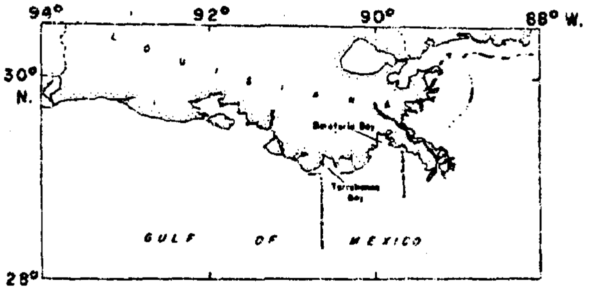


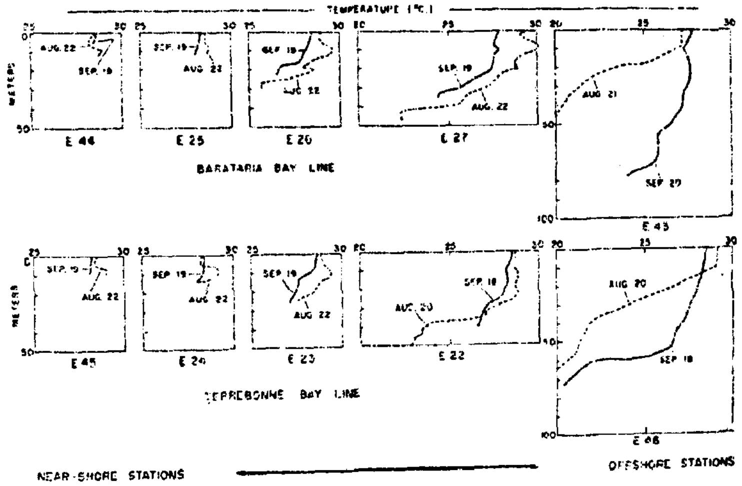
–Biofacies distribution of selected ostracod species. (Areal distribution of biofacies units is shown in Figure 7.) Biofacies units: I, offshore (middle and outer neritic, open shelf); II, inshore (paralic); including IIa, nearshore (inner neritic, open shelf); IIb, estuarine; IIc, open lagoonal; IId, interdistributary.

Fig. 15. Life zones formed by ostracod distributions in the Missisipi delta (Curtis, 1960).



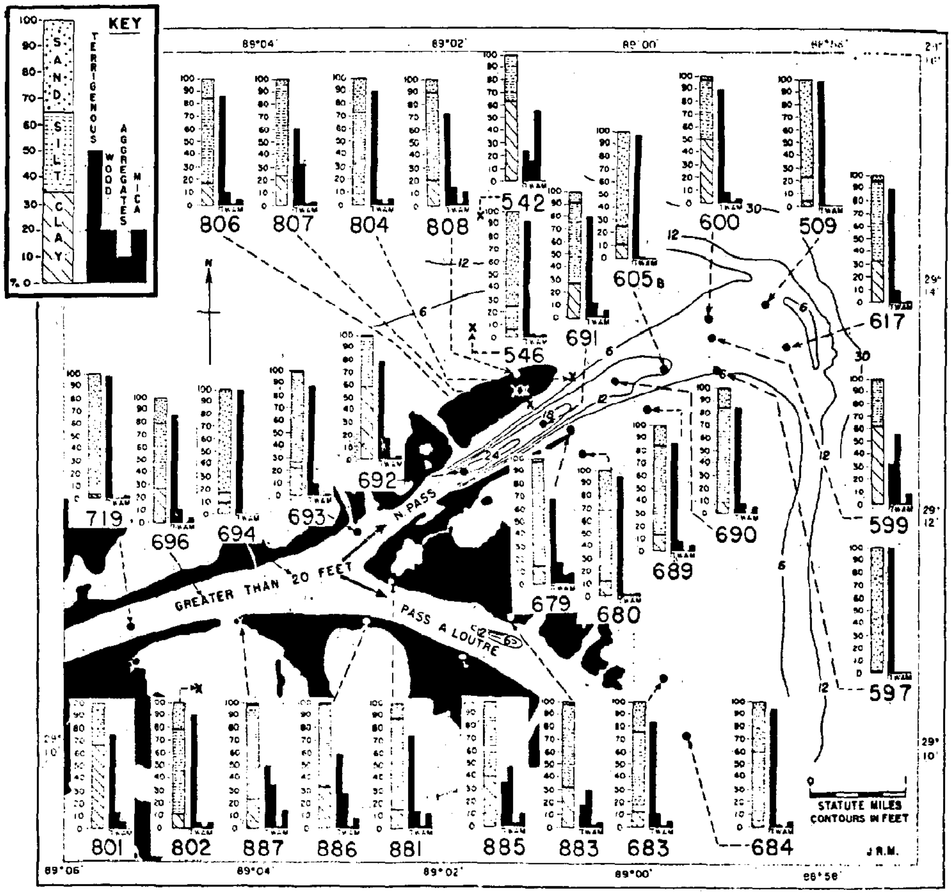
--Temperature profiles seaward from the Mississippi Delta from data gathered from the M/V Gus III and R/V Alaminos.


94°
92°
90°
88° W.
30° N.
28°
Barataria Bay
Terrebonne Bay
GULF OF MEXICO



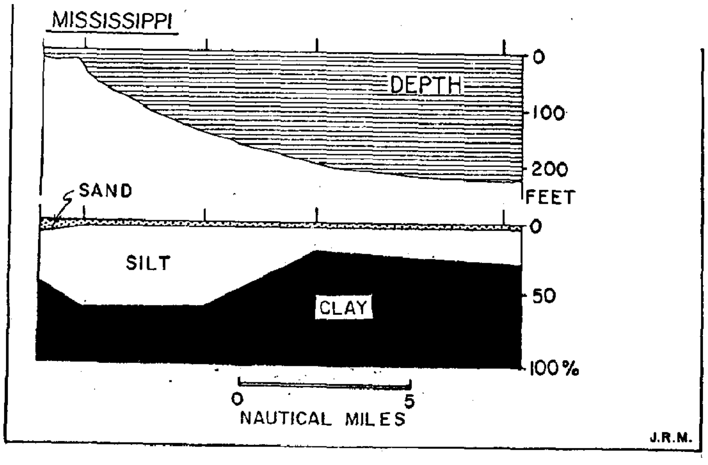
. --Temperature traces of the waters off the Mississippi Delta before and after Hurricane Betsy. The "downwelling" of warm surface waters is noted in depths greater than 50 m.

Fig. 16. Vertical temperature graphs off the Missisippi delta (Stevenson, 1966).


KEY
SAND
SILT
CLAY
TERRIGENOUS
WOOD
AGGREGATES
MICA
89°04'
89°02'
89°00'
806
807
804
808
542
546
605B
600
509
617
691
692
693
694
696
719
679
680
689
690
599
597
801
802
887
886
881
885
883
683
684
N PASS
PASS A LOUTRE
GREATER THAN 20 FEET
STATUTE MILES
CONTOURS IN FEET
J.R.M.
89°06'
88°58'
29°14'
29°12'
29°10'

–Sand-silt-clay content (left) and per cent of major constituents in the coarse fraction (right) from samples around the mouths of North Pass and Pass a Loutre, and in an interdistributary bay (Samples 801, 802). All samples except those on levees taken during low water. From Shepard, 1956a, Fig. 36.

Fig. 17. Sedimentary characteristics in the Missisippi delta (Shepard, 1960).



–Bottom profiles and sand, silt, and clay contents of sediments off major Mississippi (North Pass) and Rhone (Grand Rhone) distributaries. Sample locations are plotted horizontally from delta (left) to offshore shelf (right). Data from Shepard, 1956a, and Kruit, 1955.

Fig. 18. Sedimentary profiles of the Missisippi delta

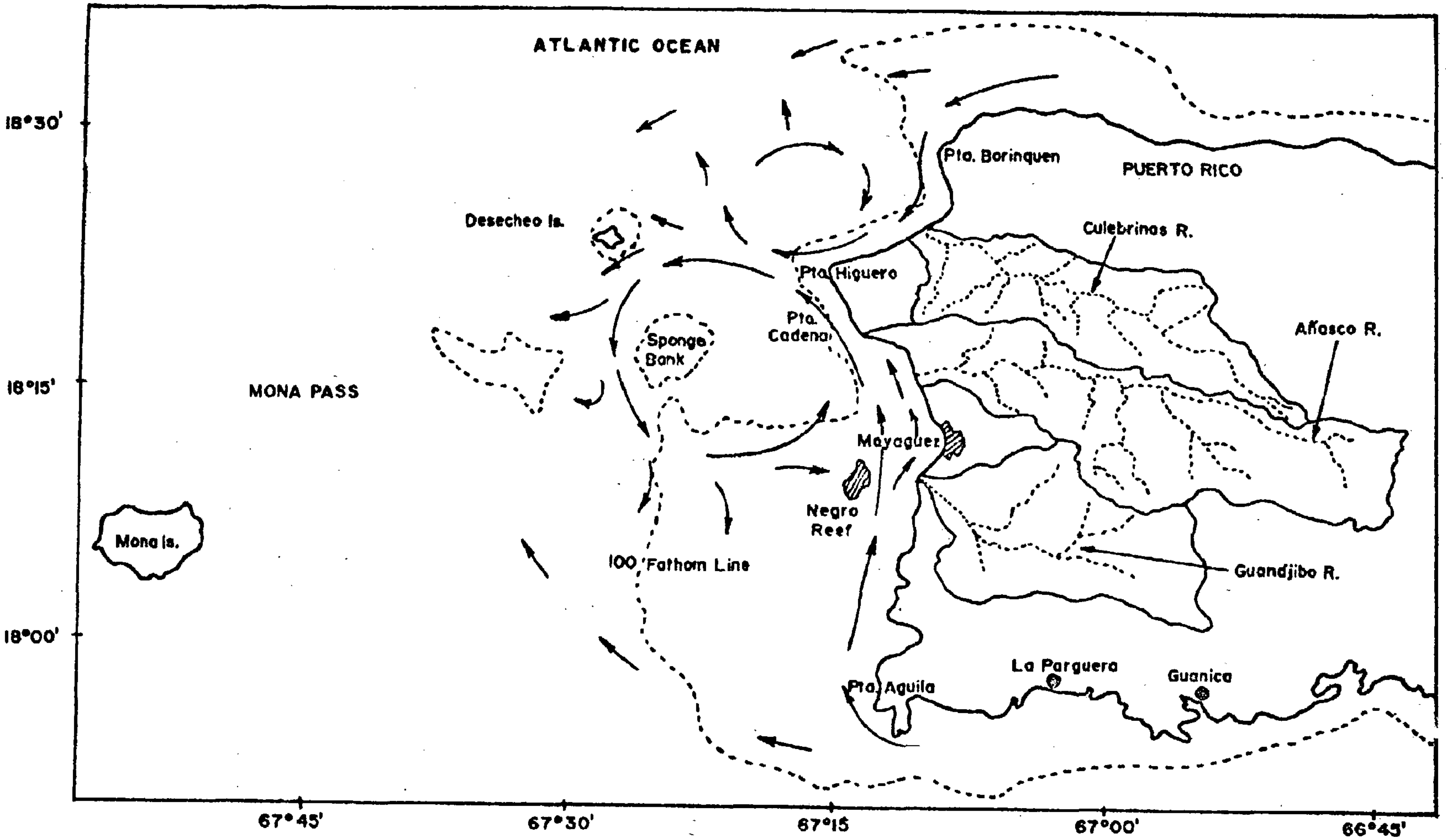
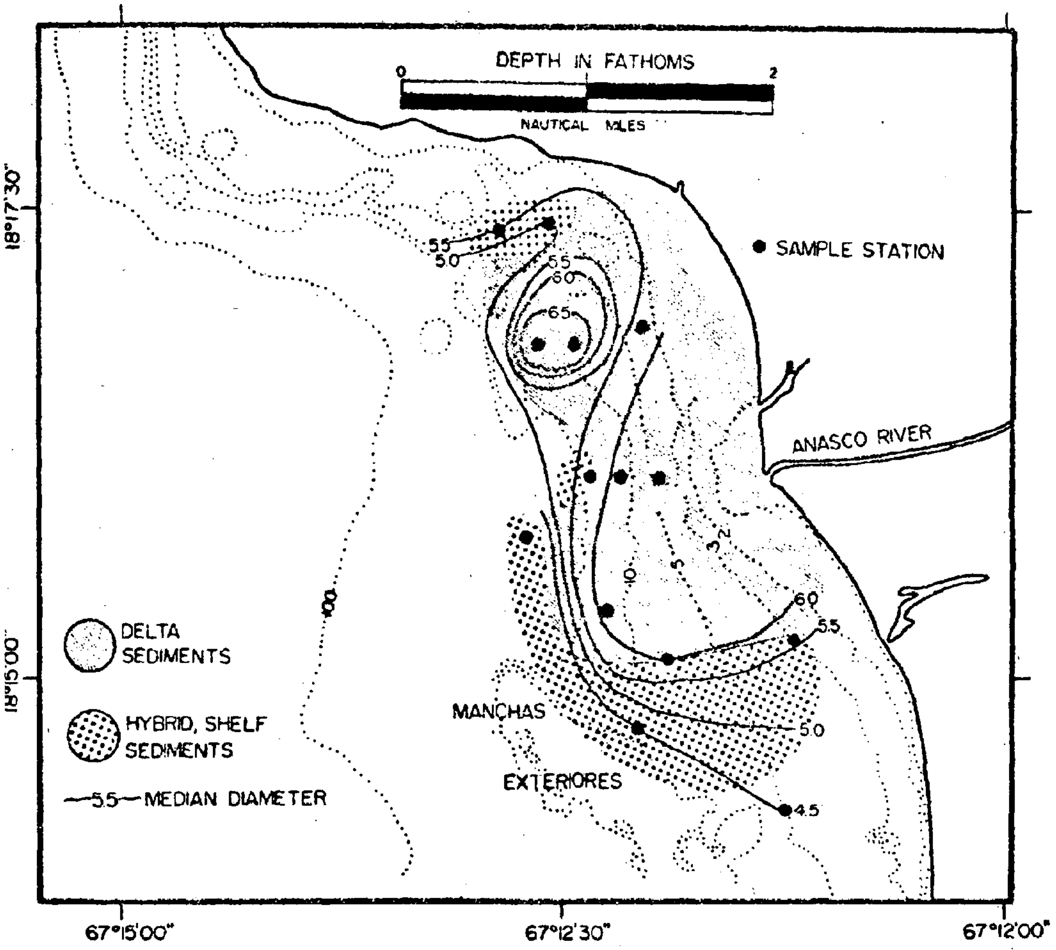
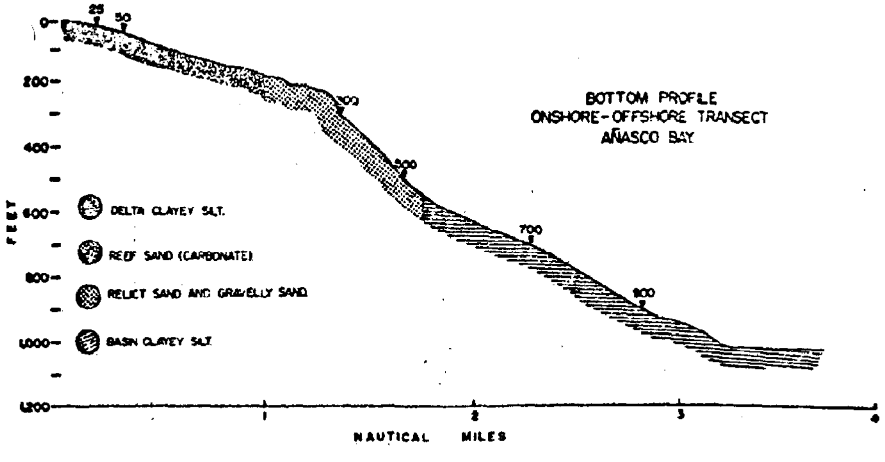

ATLANTIC OCEAN
18°30'
18°15'
18°00'
Pta. Borinquen
PUERTO RICO
Desecheo Is.
Culebrinas R.
Pta. Higuero
Pta. Cadena
Sponge Bank
Añasco R.
MONA PASS
Mayagüez
Negro Reef
Mona Is.
100 'Fathom Line
Guandjibo R.
La Parguera
Guanica
Pta. Aguila
67°45'
67°30'
67°15
67°00'
66°45'

Fig. 19. Chart of western Puerto Rico showing the watersheds of the Culebrinas, Añasco and Guanajibo Rivers. Also shown are the main current patterns along the west coast of Puerto Rico (Lowman, 1966).


DEPTH IN FATHOMS
0
2
NAUTICAL MILES
18°17'30"
18°15'00"
67°15'00"
67°12'30"
67°12'00"
SAMPLE STATION
AÑASCO RIVER
DELTA SEDIMENTS
HYBRID, SHELF SEDIMENTS
5.5 MEDIAN DIAMETER
MANCHAS
EXTERIORES
5.5
5.0
5.5
6.0
6.5
6.0
5.5
5.0
4.5
100
10
5
3
2



Edo profile and bottom sediments on a line due east from the Añasco River Mouth.

Fig. 20. Sedimentary patterns of the Añasco River delta, Puerto Rico (Lowman, Phelps, Ting, et. al., 1967).

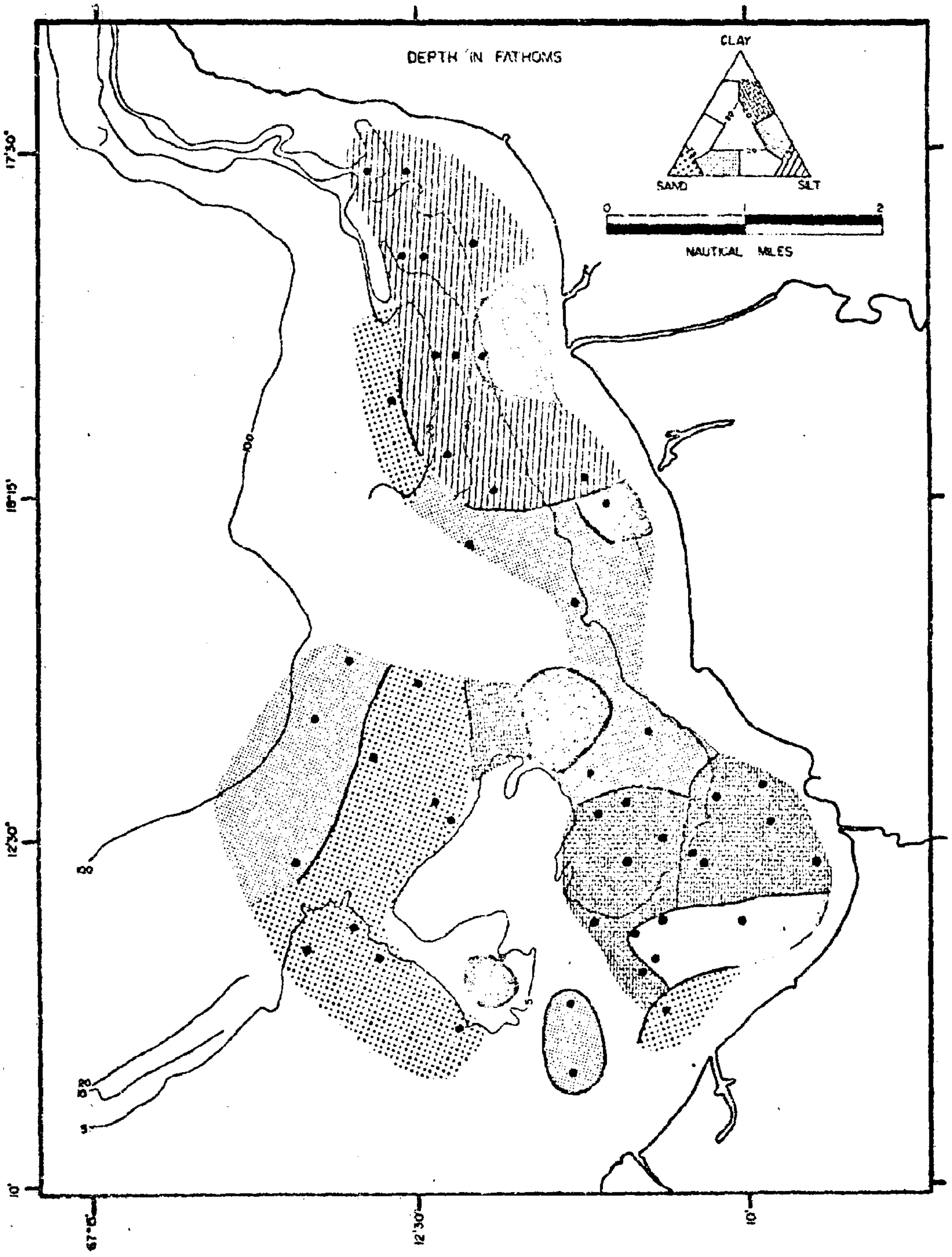

DEPTH IN FATHOMS
CLAY
SAND
SILT
0
1
2
NAUTICAL MILES
17'30"
18°15'
12'30"
10'
67°15'
12'30"
10'
100
10
20
5

Fig. 21. Sedimentary Facies of Mayaguez and Añasco Bays based on sand-silt-clay percentages. (Lowman, Phelps, Ting, et. al.,1967).

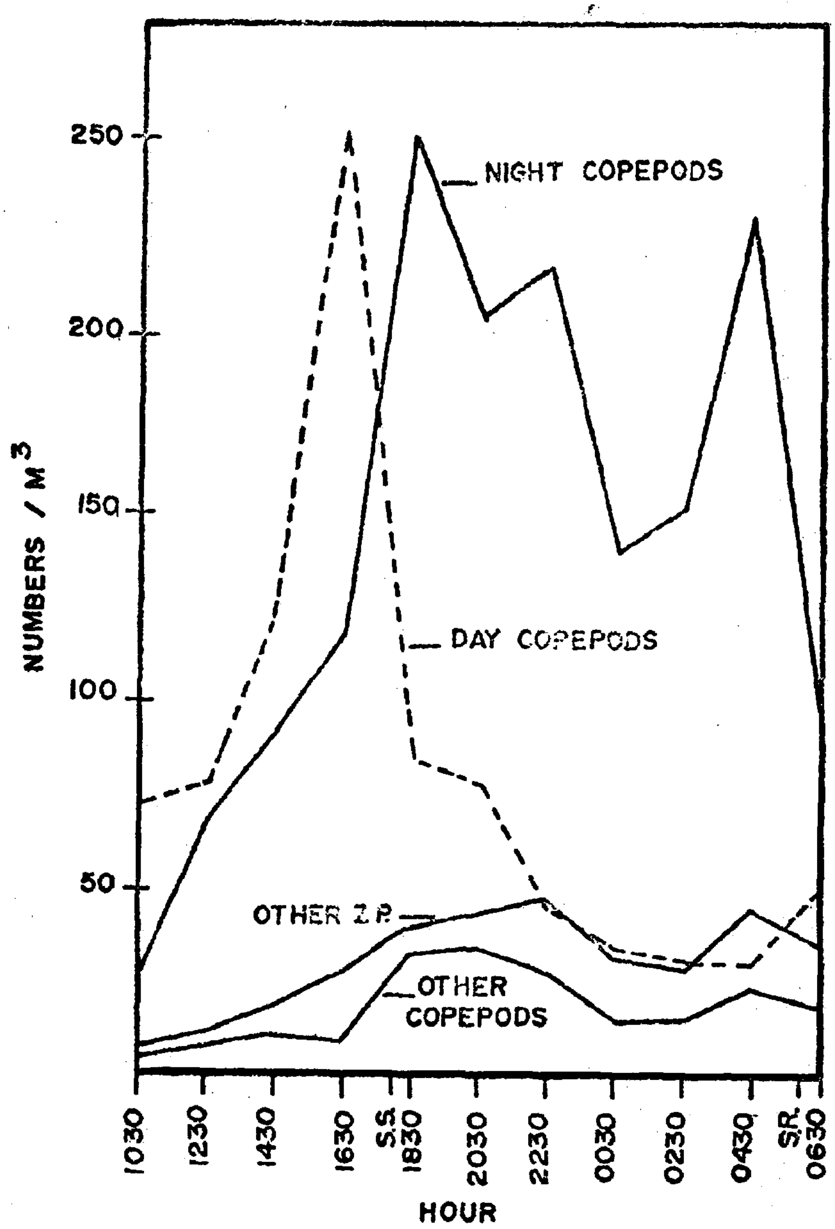
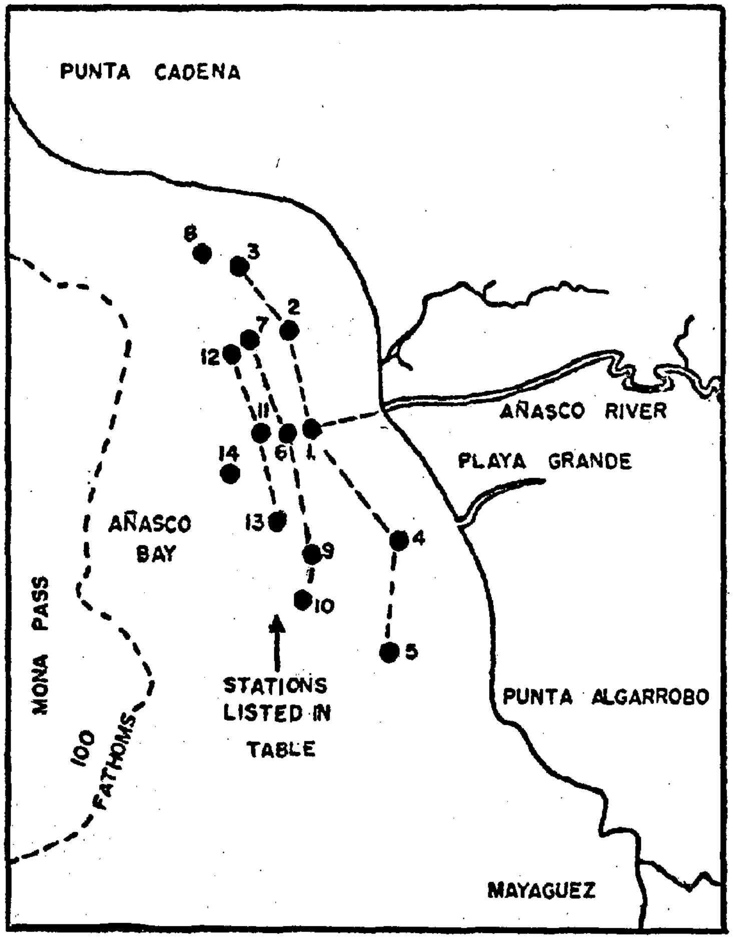


Fig. 22. Abundance of the more-numerically important copepods whose maximum concentrations occurred in the day or night plus all other copepods and total zooplankton, other than copepods, are plotted at hour sampled.

(Lowman, Phelps, Ting, et. al., 1967).

Station	Depth	Biomass	MgFe/gmDWt/M^2	MgZn/gmDWt.M^2	MgSc/gmDWt/M^2	MgSm/gmDWt.M^2
1	25'	1.70	7.7	310	2.9	0.5
4	25'	4.53	17.6	470	5.2	1.4
2	25'	3.91	6.4	540	4.0	1.1
6	50'	10.39	14.	150	6.8	1.3
11	75'	16.41	6.4	9.2	4.9	0.1
7	50'	2.06	1.6	90	1.6	0.8
13	50'	2.38	7.0	110	2.9	0.50
12	50'	5.92	2.4	50	1.7	0.2
9	50'	4.44	8.8	85	5.0	0.50
10	50'	1.18	2.1	40	1.0	0.2
14	125	1.93	13.	140	5.5	1.5
3	25'	19.43	3.7	490	5.2	0.7
5	25'	15.44	8.6	640	5.5	1.1
8	50'	12.70	4.6	30	5.3	0.2


PUNTA CADENA
8
3
2
7
12
11
6
1
14
13
9
4
10
5
AÑASCO RIVER
PLAYA GRANDE
AÑASCO BAY
MONA PASS
100 FATHOMS
STATIONS LISTED IN TABLE
PUNTA ALGARROBO
MAYAGUEZ

Total biomass per square meter in the top 8 centimeters at 14 stations off the Añasco River (see inset fig.). Also shown are the total amounts of iron, zinc, scandium and samarium incorporated into the benthic infauna.

Fig. 23. Distribution of biomass and 4 trace elements off the Añasco River delta of western Puerto Rico (Lowman, Phelps, Ting, and Escalera, 1966).

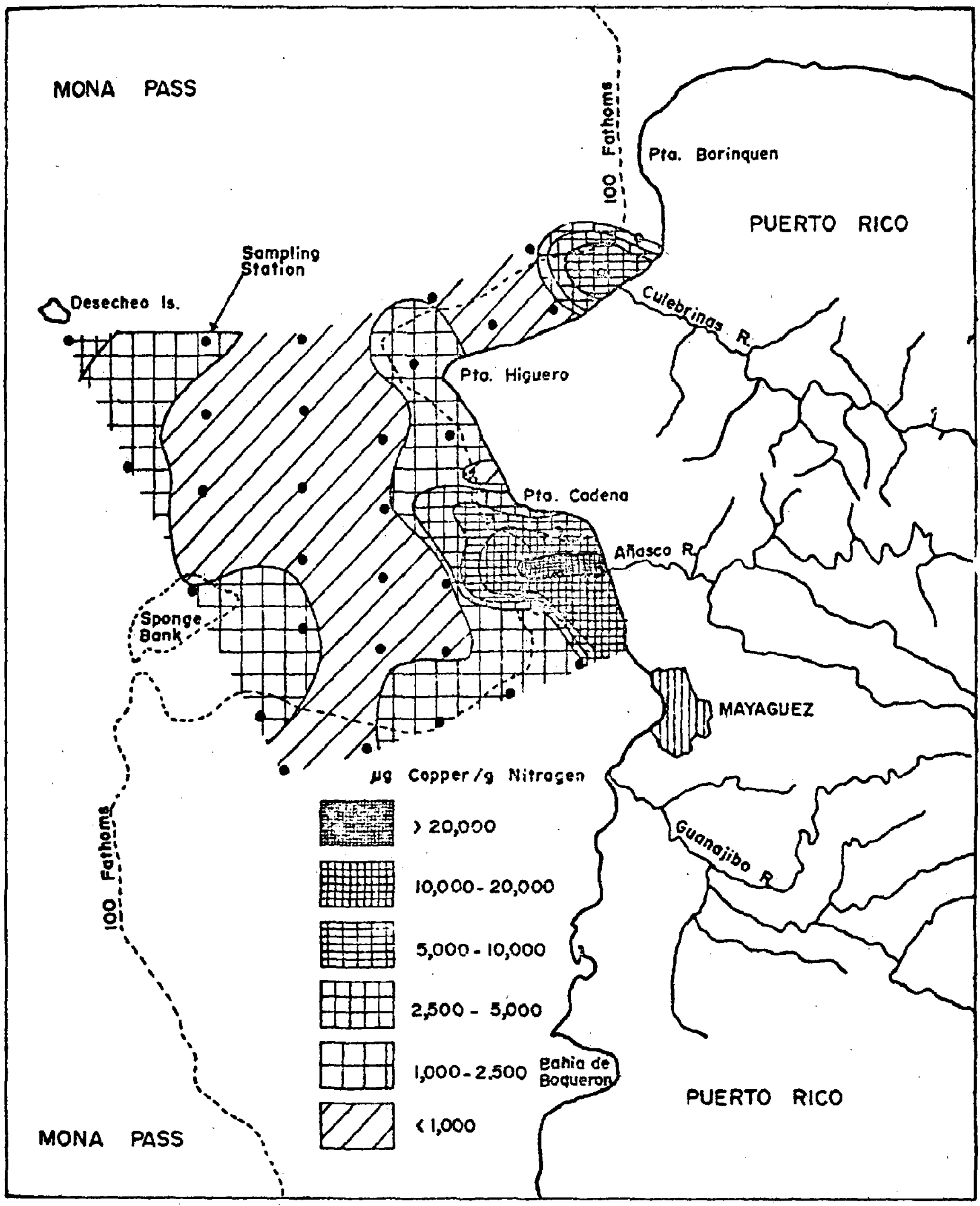

MONA PASS
100 Fathoms
Pta. Borinquen
PUERTO RICO
Sampling Station
Desecheo Is.
Culebrinas R.
Pta. Higuero
Pta. Cadena
Añasco R.
Sponge Bank
MAYAGUEZ
µg Copper/g Nitrogen
> 20,000
10,000 - 20,000
5,000 - 10,000
2,500 - 5,000
1,000 - 2,500
< 1,000
Guanajibo R.
Bahia de Boqueron
100 Fathoms
PUERTO RICO
MONA PASS

Fig. 24. Distribution pattern of copper per gram of nitrogen in mixed phyto- and zooplankton collected off the west coast of Puerto Rico (Lowman, Phelps, Ting, and Escalera, 1966).

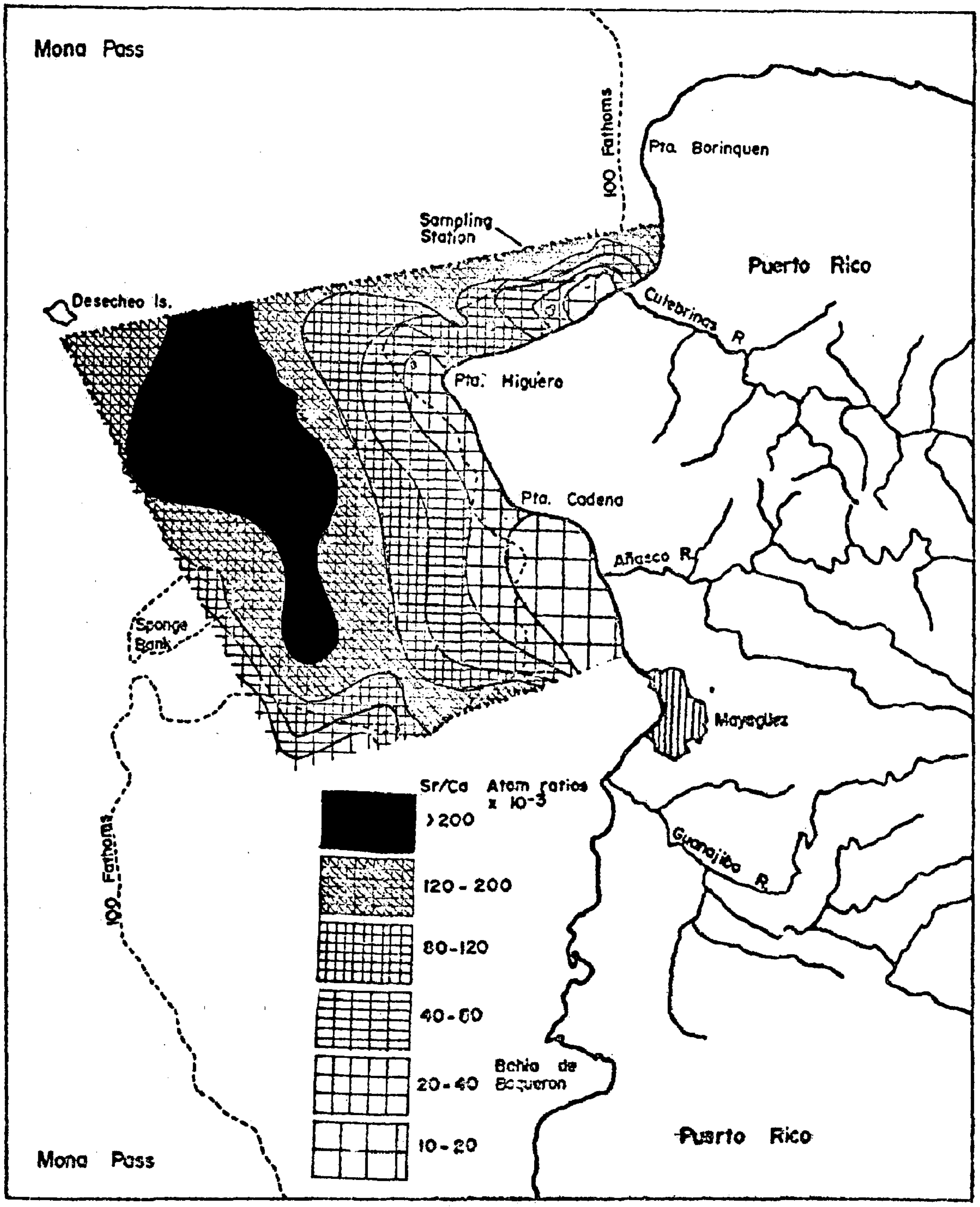

Mona Pass
100 Fathoms
Pta. Borinquen
Sampling Station
Puerto Rico
Desecheo Is.
Culebrinas R.
Pta. Higuero
Pta. Cadena
Añasco R.
Sponge Bank
Mayagüez
Sr/Ca Atom ratios x 10-3
>200
120-200
80-120
40-80
20-40
10-20
Guanajibo R.
100 Fathoms
Bahia de Boqueron
Puerto Rico
Mona Pass

Fig. 25 Strontium/calcium ratios in mixed phyto- and zooplañkton off the west coast of Puerto Rico

(Lowman, Phelps, Ting, and Escalera, 1966).

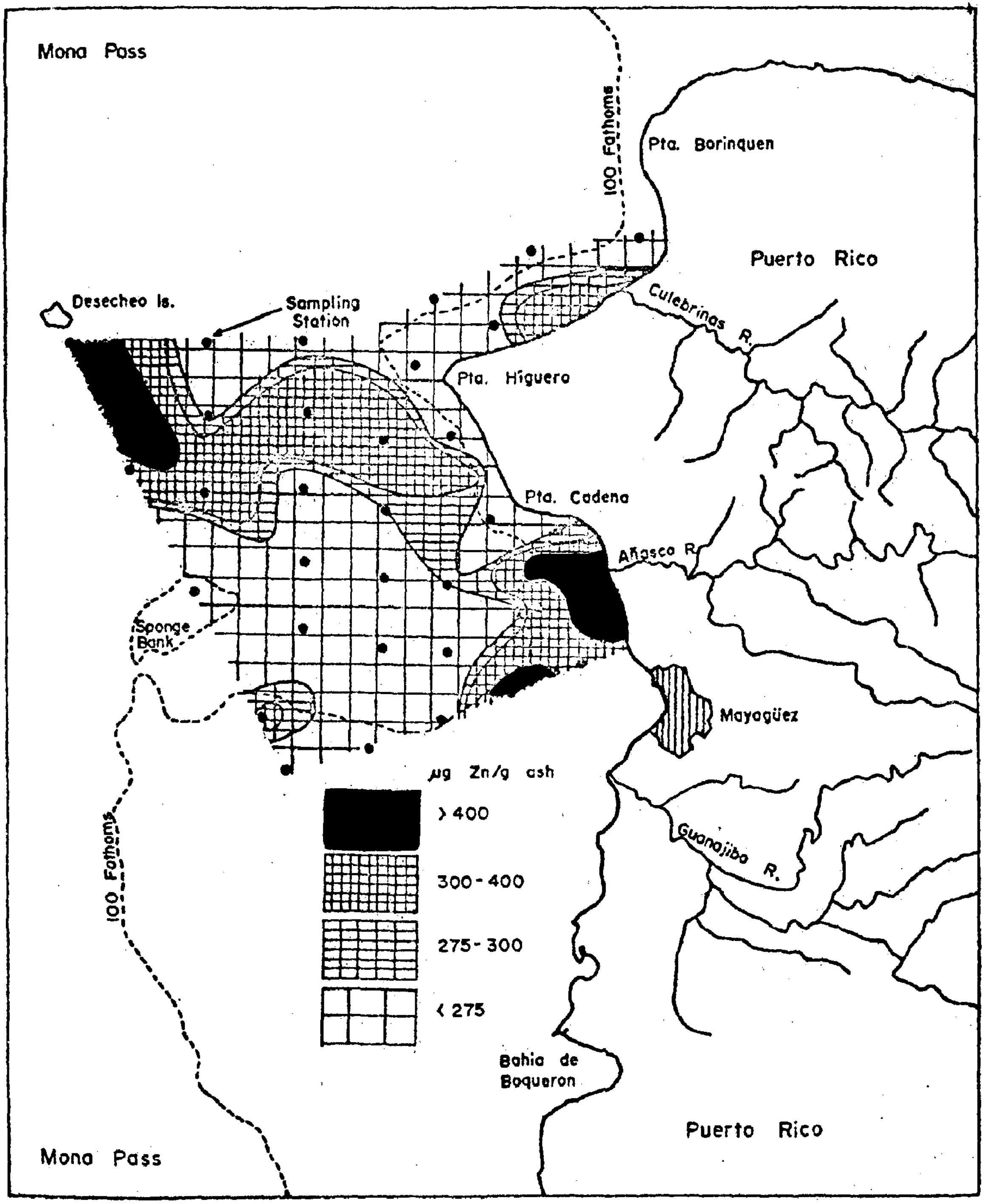

Mona Pass
100 Fathoms
Pta. Borinquen
Puerto Rico
Culebrinas R.
Desecheo Is.
Sampling Station
Pta. Higuero
Pta. Cadena
Añasco R.
Sponge Bank
Mayagüez
µg Zn/g ash
> 400
300 - 400
275 - 300
< 275
Guanajibo R.
100 Fathoms
Bahia de Boqueron
Puerto Rico
Mona Pass

Fig. 26. Distribution pattern of zinc per gram of ash in mixed phyto- and zooplankton collected off the west coast of Puerto Rico

(Lowman, Phelps, Ting, and Escalera, 1966).

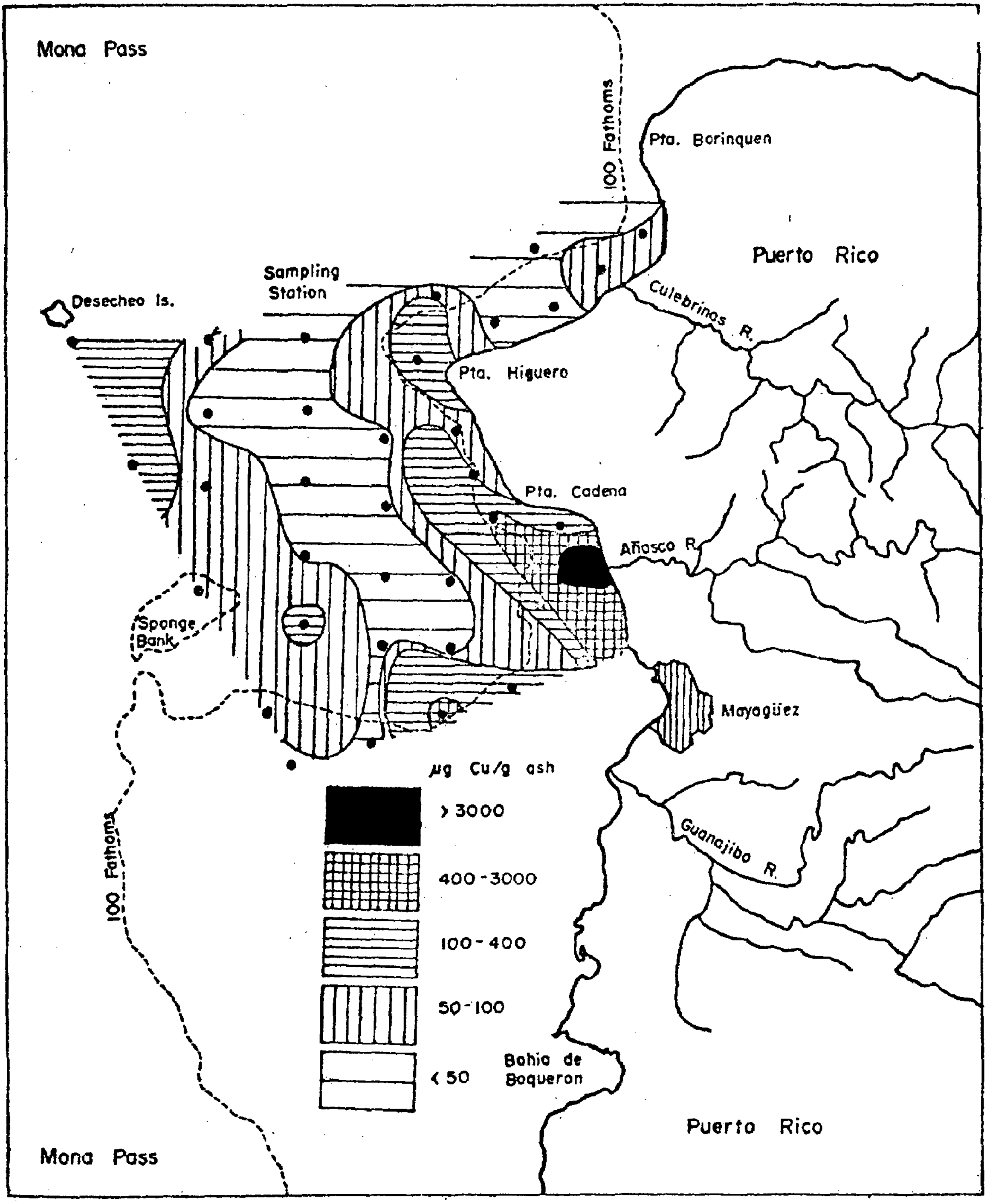

Mona Pass
100 Fathoms
Pta. Borinquen
Puerto Rico
Culebrinas R.
Sampling Station
Desecheo Is.
Pta. Higuero
Pta. Cadena
Añasco R.
Sponge Bank
Mayagüez
µg Cu/g ash
> 3000
400 - 3000
100 - 400
50 - 100
< 50
Guanajibo R.
100 Fathoms
Bahia de Boqueron
Puerto Rico
Mona Pass

Fig. 27. Distribution pattern of copper per gram of ash in mixed phyto- and zooplankton collected off the west coast of Puerto Rico (Lowman, Phelps, Ting, and Escalera, 1966).

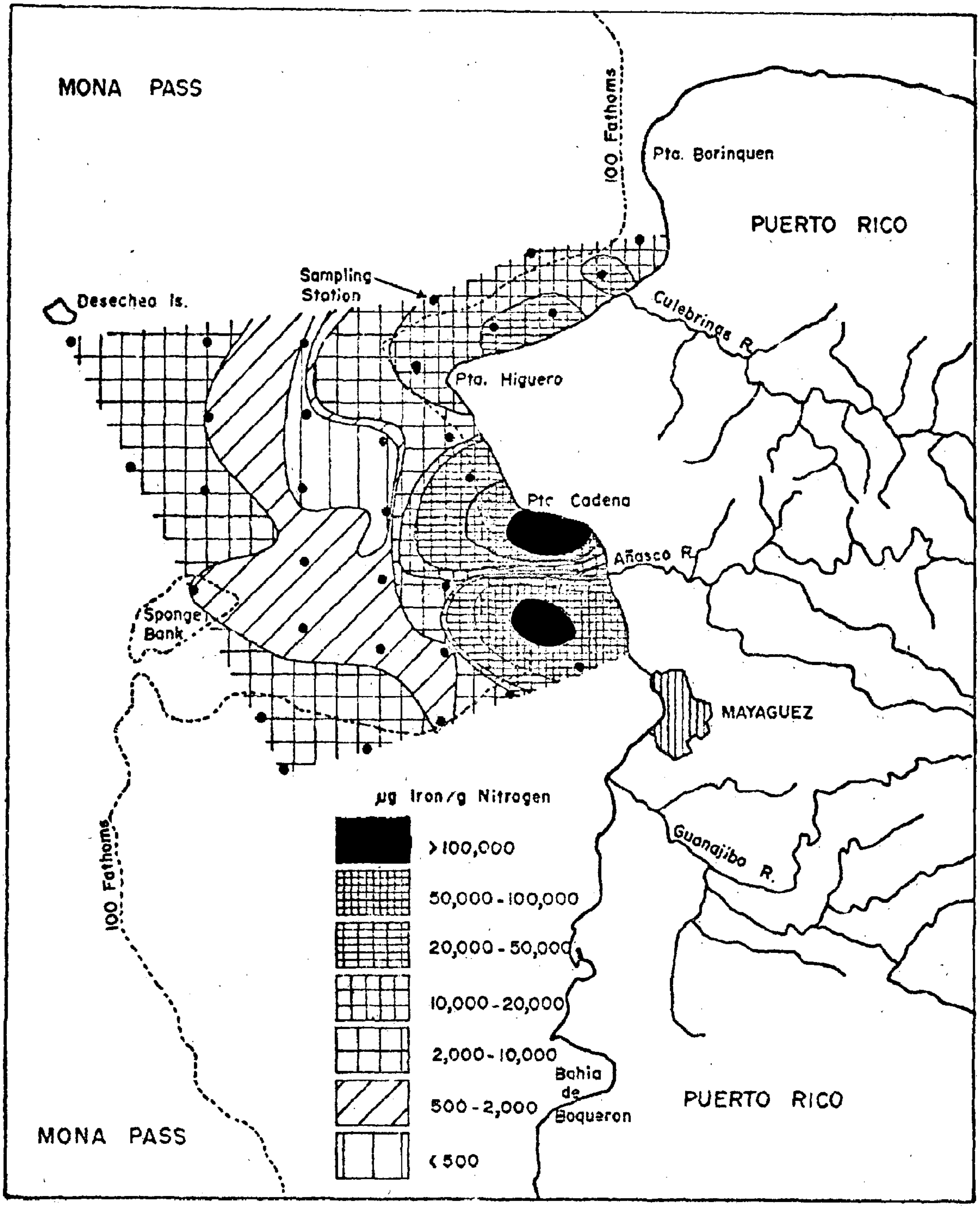
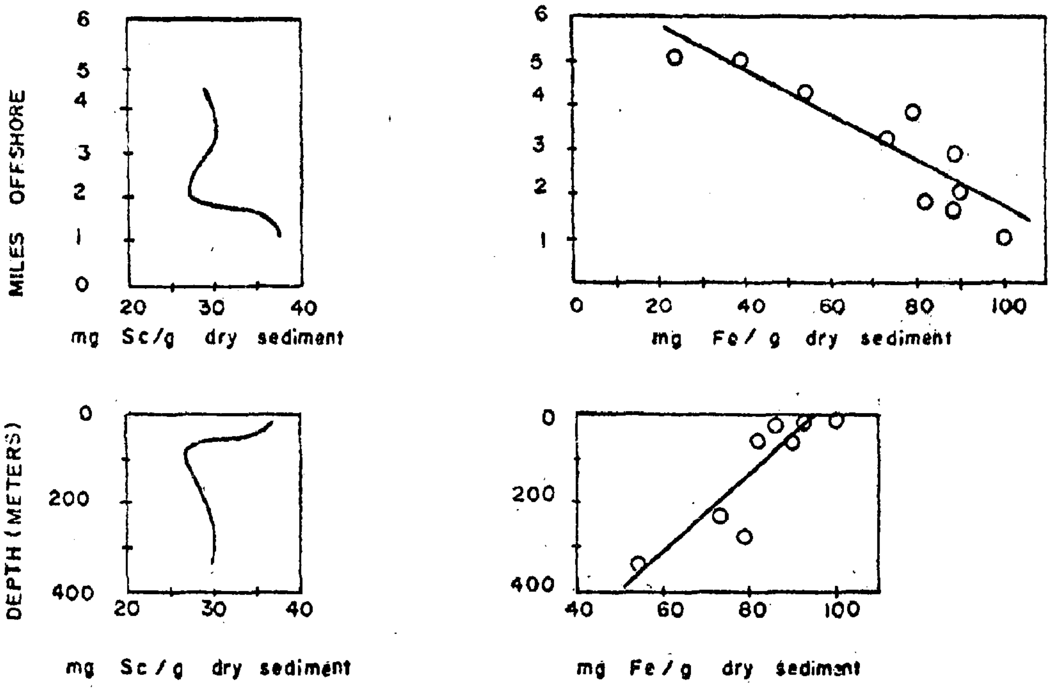

MONA PASS
100 Fathoms
Pta. Borinquen
PUERTO RICO
Sampling Station
Desecheo Is.
Culebrinas R.
Pta. Higuero
Pta Cadena
Añasco R.
Sponge Bank
MAYAGUEZ
µg Iron/g Nitrogen
>100,000
50,000 - 100,000
20,000 - 50,000
10,000 - 20,000
2,000 - 10,000
500 - 2,000
<500
Guanajibo R.
100 Fathoms
Bahia de Boqueron
PUERTO RICO
MONA PASS

Fig. 28. Distribution pattern of iron per gram of nitrogen in mixed phyto- and zooplankton collected at 37 stations during a 10 hour period off the west coast of Puerto Rico (Lowman, Phelps, Ting, and Escalera, 1966).



Variation of scandium and iron with distance from the outflow of the Añasco River and with sampling depth.

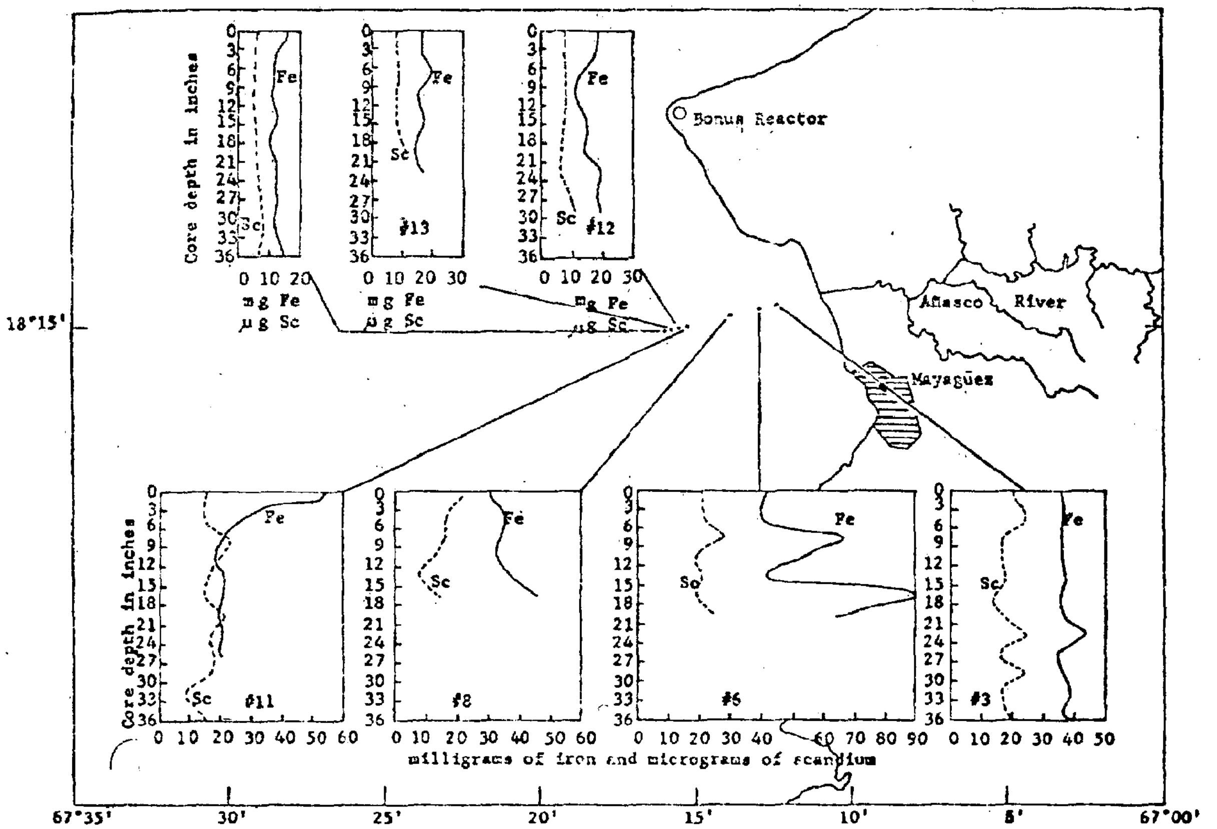

Core depth in inches
Fe
Sc
#13
#12
#11
#8
#6
#3
mg Fe
µg Sc
Bonus Reactor
Añasco River
Mayagüez
milligrams of iron and micrograms of scandium
18°15'
67°35'
30'
25'
20'
15'
10'
5'
67°00'

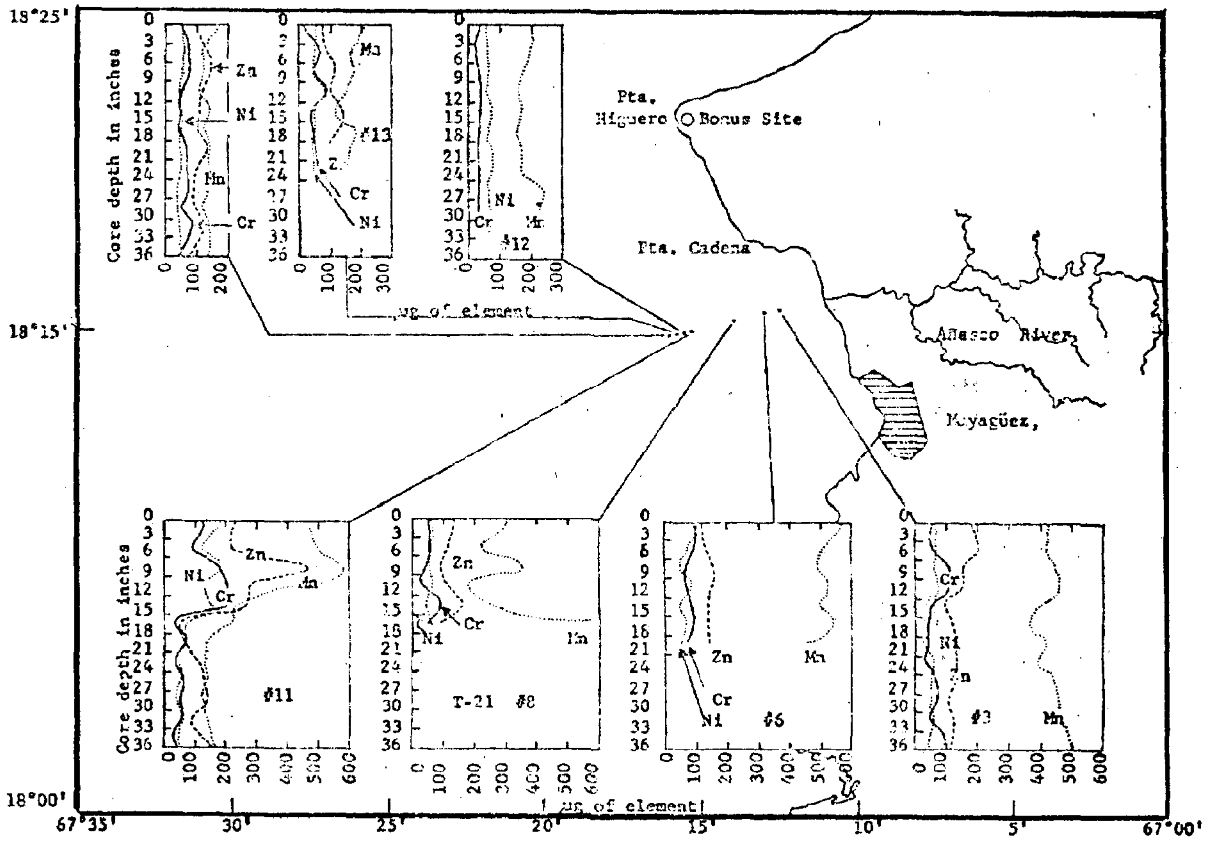
Fig. 5

Distribution of iron and scandium, with depth, in marine sediments taken off the west coast of Puerto Rico. The amounts of iron and scandium in the sediments were inversely related to distance from shore.

Fig. 29. Trace elements in the Añasco River delta (Lowman, Quinones. Miro. Padovani, et al., 1966).

ANALYSES OF MAGNESIUM, STRONTIUM, CALCIUM, ZINC, NICKEL, CHROMIUM, MANGANESE, IRON AND SCANDIUM IN SEDIMENTS TAKEN OFF THE AÑASCO RIVER WITH AN ORANGE-PEEL GRAB

Sample No.	Distance off-shore	Depth (meters)	*Micrograms of element per gram of dry sediment*								
			Mg	Sr	Ca	Zn	Ni	Cr	Mn	Fe	Sc
1	1.2	8	10,000	24	1,400	120	52	55	710	44,000	25
2	1.4	22	—	—	—	140	56	65	400	38,000	25
4	1.9	60	16,000	110	24,000	150	65	57	600	48,000	19
5	2.0	65	17,000	110	19,000	150	56	52	650	51,000	—
7	2.9	190	14,000	330	44,000	150	66	77	390	32,000	20
9	3.3	230	15,000	400	57,000	140	66	44	400	30,000	14


18°25'
18°15'
18°00'
67°35'
30'
25'
20'
15'
10'
5'
67°00'
Core depth in inches
Zn
Ni
Mn
Cr
#13
#12
#11
T-21 #8
#6
#3
μg of element
Pta. Higuero
Bonus Site
Pta. Cadena
Añasco River
Mayagüez

Distribution of manganese, chromium, and nickel, with depth, in marine sediments taken off the west coast of Puerto Rico. The levels of manganese in the sediments were inversely related to distance from the shore. The larger amounts of manganese, zinc, chromium, and nickel in sample No. 11 probably reflect the effect of a submarine slide upon the sediments in this area.

Fig. 30. Trace element distribution in sediment cores in the Añasco River delta, Puerto Rico (Lowman, Quinones, Miro, Padovani, et. al.,1966).

Other Examples

Sedimentary deltas have a worldwide distribution. In many areas deltas are the sites of cities, harbors, or important agricultural lands, so they have been studied extensively. In the United States deltaic regions are much more insulated from the main population. The small deltas of the Rio Grande, Brazos, and Appalachicola rivers have been studied extensively, as have numerous small deltas that presently are building into the lagoons and estuaries of the Texas and Gulf Coast. Other deltas, more or less well known, are the Colorado River delta at the head of the Gulf of California, the San Joaquin delta at the head of San Francisco Bay, and the Fraser River Delta near Vancouver, British Columbia just beyond the United States boundary. There are several important deltas in Alaska, including that of the Yukon and the Kuskoquim. The east coast United States has no active deltas, except some very small ones at the heads of estuaries that characterize this coast. Before the Santee River in South Carolina was diverted into Charleston harbor it was building a delta into the Atlantic Ocean and the cuspate form of the old Santee delta can be seen on maps of this region.

Some famous deltas in other parts of the world include those of the Mediterranean Sea--the Nile, the Po, and the Rhone. The Netherlands and Danish archipelago is built upon the deltaic system of the Rhine-Scheldt-Meuse system. In Africa the delta of the Niger has a classic form, and in South America the delta of the Orinoco in Venezuela has been much studied. Some of the great deltas of the world are found in Asia, but these are less well known to westerners. Some important ones are the deltas of the Ganges and Irrawaddy in India, the Hwang Ho in China, and there are many others. The illustrations of deltaic environments that follow have been taken from the best studied of these deltas.

DISCUSSION

Deltas have a characteristic two dimensional form (such as that of the Nile shown in Figure 1a, from which the name "delta" derives), a three dimensional structure (Figure 1b), and a characteristic mode of evolution through time. When the supply of river borne sediment exceeds the rate of removal, deltas intrude upon normal estuarine or marine environments in the course of time. In this sense the sediment pollutes the environment, but this must be considered an expected outcome wherever the delta advances rapidly. If the forces of marine erosion overcome those of sediment supply, the front of the delta is cut back, beach deposits form along the shoreline, and the stage is set for a new phase of advance. Figure 2 shows the structure that results after two periods of advance interrupted by one of retreat. Because of the high sedimentation rate, the sediment that accumulates is very loose and contains large amounts of water. As the sediment consolidates, the surface of the delta sinks at rates that vary from 0.05 to 0.17 feet per year. This phenomenon poses special land use problems in deltaic areas. Figure 3 shows the magnitude of this problem in a heavily populated area in Japan. Subsidence also gives rise to special kinds of estuaries that exist on the surface of the delta (see below). The water that is forced out of deltaic sediments during their compaction migrates to porous sand strata within the deltaic mass, produces remarkable conditions of hydrostatic forces within the subsurface, and generally causes unique problems of water supply and use in the area of the delta.

The general form of shallow water deltas is shown in Figure 1. The visible part of the Nile delta has a generally arcuate shape in two dimensions, both above sea level and below. Between Cairo and the sea the Nile River breaks up into a number of smaller branches, called distributaries. Each distributary consists of a river channel contained within two bordering levees. Between distributaries are extensive, low, marshy areas that are subject to extensive flooding, both from the river and from the sea. Subsidence produces interdistributary estuaries or bays in such areas (Figure 4). The profile across the Nile delta (Figure 1b) shows the various natural regions into which the delta can be subdivided. The subaerial topset plain is constructed of freshwater river sediments, largely sands. The subaqueous topset plain--often referred to as the delta front platform--consists of predominantly sandy deposits constructed during the abrupt interaction between river and ocean currents that occurs at the very edge of the delta. The foreset slope, or pro-delta slope, contains largely silty deposits that drop out when the turbid river water flows out upon the sea and loses its momentum. The foreset slope is a very gently incline surface with a slope of 0.3 to 1.0 per cent. Beyond the foreset slope is a very flat region in deep water where fine clays accumulate slowly. This is called the bottomset plain. The Mississippi delta is building into deep water, rather than into a shallow sea, and its surface form is quite unusual. Even so, the same natural regions have been recognized, as Figure 5 shows. The topset plain and the bottomset plain occupy the largest areas in a delta, but about 75 per cent of the sediment deposition takes place on the narrowly restricted foreset slope. If, due to rapid sedimentation, the foreset slope builds out too rapidly and becomes over steepened (slopes greater than 1 per cent), slumping occurs and sediment is moved en mass down the slope to the bottomset plain. Such activity gives rise to channeled topography along the foreset slope adjacent to active distributaries, such as appear in Figure 6. Such activity must be inimical to bottom dwelling life to an even greater degree than the high sedimentation rate and turbidity that characterize deltaic environments generally.

The environments in front of an advancing delta are estuarine in the sense that fresh and salt water mix in them, but they are a very special kind of estuarine environment. The transition between freshwater and sea water is more abrupt in marine deltas than in most estuarine environments. Where a delta protrudes into an enclosed bay or lagoon, the transition from fresh water to the water of the bay or lagoon is more abrupt than usual. The salinity of the bottom water immediately in front of a delta is nearly that of the adjoining sea or bay water, even though large volumes of fresh water flow out from the river at the surface. This is because the forces that tend to mix fresh and salt water (the tidal currents) normally are weak in front of deltas. In fact, this factor is a major control on the occurrence and distribution of deltas. Where there are strong tidal forces, the sediment supplied by rivers is eroded and removed; where there are weak tidal forces, the sediment deposits and forms deltas. As a result of the weak mixing forces, the vertical salinity gradient in front of a delta is very marked. Virtually fresh water flows out at the surface, and sensibly marine water intrudes along the bottom over the delta front platform and into the distributary channels. Organisms that live on the bottom must be adapted to relatively saline water. The position of the leading edge of the saline water is determined by the hydrostatic force exerted by the freshwater flow. When the flow is low, the saline water penetrates far up the distributary channels; when the freshwater flow is large, salt water is flushed out of the channels and across the delta front platform. From the ecological point of view, this means that environments in the distributary channels and on the delta front platform are subject to extreme salinity shocks that correlate with the freshwater discharge. The vertical distributions of salinity during a high and a low stage at the mouth of the Mississippi River are shown in Figure 7. The intrusion and extrusion of salt water in the river channel at different stages show clearly. These diagrams also show the strong contrast between surface and bottom salinities. Of course, examples are known where deltas are building seaward in the face of strong tidal currents. The Rhine-Scheldt delta complex in the Netherlands is an example. Here the deltaic distributary channels are much more typically estuarine in having a salinity gradient that is stretched out along the bottom. The bottoms of such distributaries are less subject to extreme stresses due to salinity shocks.

The distributary channels, the delta front platform, and the pro-delta slope are all subject to extreme temperature shocks, by virtue of the fact that river water temperatures nearly always contrast strongly with that of ocean water. In temperate climates the high discharge period of the river brings very cold water to the delta margins, since this discharge occurs in early spring. At other times of year and in other latitudes the thermal contrasts are not so severe. Figure 8 shows how the difference in surface water temperatures in the Gulf of Mexico region is greatest in the vicinity of the Mississippi delta and other sources of land drainage.

The environments marginal to the delta are regions of high turbulence, another important stress that affects the indigenous fauna. Since water depths in the distributary channels and the delta front platform are small (20 feet or less), local wind waves or swells that approach from the sea stir the bottom. Strong currents from the river and those from the tides also sweep over these shallows creating a high degree of turbulence almost continuously.

One of the effects of high turbulence is a continuously high oxygen supply in the surface waters. At depths below the surface and particularly on the bottom on the foreset slope, however, serious oxygen depletion can occur because of the high organic content of the sediment, the extreme vertical density stratification, and the relatively slow rate of water renewal from the sea source. On the other hand, beyond the foreset slope where the rate of supply or organic rich sediment is low, highly oxidizing conditions become re-established.

The freshwater discharge of the river brings both nutrients and suspended sediment to the margin of the delta. In most deltas the quantity of freshwater discharged varies considerably seasonally. In temperate regions the maximum corresponds to the early spring runoff period. In mediterranean climates there often are two maximum discharge seasons. In tropical deltas an annual flood corresponds to the rainy season. Turbid water, even though highly charged with particulate matter and often colder than the sea water, has a relatively low density and is forced to flow out on the sea surface. The momentum of the river carries the turbid freshwater flow for several miles beyond the delta margin--as much as 50-60 miles for spring floods in a large river. The freshwater gradually assimilates the surface sea water as it is propelled along. Thus there is a horizontal salinity gradient at the surface in front of the delta (Figure 13). (Such strong horizontal salinity gradients do not exist along the bottom in front of deltas.)

The suspended sediment concentration at the surface in front of a delta ranges from 10—100 milligrams per liter. This is very turbid compared to sea water where the suspended matter is less than 1 milligram/liter, including plankton. The high concentrations of suspended particles in the surface layer block penetration of sunlight. Even in very shallow depths organisms must be prepared to live on the bottom in absolute darkness. The bottom waters may be relatively free of particles but they are shaded from any light.

The sedimentation rates in the vicinity of distributaries of the Mississippi and Rhone (France) deltas are as high as 1 foot per year and in some areas even more. These rates are normal for large deltas. They are probably somewhat unusual for smaller ones, but a rate only half as great would still pose quite a survival problem for all but the most mobile of benthic invertebrates. On the delta-front platforms the deposition is much slower, on the order of 0.1 foot per year. On the bottomset plain the rates are very slow, perhaps 0.01 foot per year, or even less. On the one hand the continuous rain of particles from above causes a survival problem, but on the other hand, it brings an unfailing supply of nutrient rich food. Thus the environment can support large numbers of the particular species that can survive conditions of rapid sedimentation. Mackenzie, Garrels, Bricker, and Bickley (1969) show suspended clays controlling water content on one nutrient element (Fig. 31). Thomas and Simmons (1960) give productivity data in Tables 2 and 3.

The surface waters in front of deltas are relatively rich in nutrients that are brought to the sea in the freshwater. Their abundance fluctuates with changes in the amount of freshwater flow. Because of the abundant nutrient supply a large standing crop of plankton can be supported in these surface waters. The most abundant forms are diatoms and copepods. The numbers of diatoms decrease away from the front of the Po delta (Italy) from about 32,000 per liter to about 22,000 per liter in a distance of 30 miles. Within the next 100 miles the diatoms decrease in number to about 800 per liter, while the effects of freshwater as measured by the salinity virtually disappear. It is probably not only the inorganic nutrients that provide for the high standing crop near the delta, but organic nutrient substances carried by the freshwater apparently influence the abundance and distribution of

Table 2. Phytoplankton, nutrients and photosynthetic productivity measurements in the Missisippi delta Thomas and Simmons(1960).

MEAN AND MEDIAN PHOSPHATE CONCENTRATIONS AT THREE SEASONS AND IN VARIOUS AREAS OF THE DELTA

Area		*Fall Months*	*February*	*May*
River	Mean PO_4 (μgm-atom/L)	1.91	1.20	0.81
	Median PO_4 (μgm-atom/L)	1.03	1.09	0.38
	Number of determinations	4	17	3
Plume	Mean PO_4 (μgm-atom/L)	1.17	1.68	1.30
	Median PO_4 (μgm-atom/L)	0.58	1.06	0.92
	Number of determinations	19	32	11
Gulf	Mean PO_4 (μgm-atom/L)	0.32	—	1.26
	Median PO_4 (μgm-atom/L)	0.35	—	0.64
	Number of determinations	10	—	28
Breton Sound	Mean PO_4 (μgm-atom/L)	1.67	1.30	1.21
	Median PO_4 (μgm-atom/L)	1.66	1.30	1.21
	Number of determinations	4	2	1
Blind Bay	Mean PO_4 (μgm-atom/L)	3.70	3.38	—
	Median PO_4 (μgm-atom/L)	3.70	2.45	—
	Number of determinations	1	4	—

MEAN SURFACE PHYTOPLANKTON PRODUCTION IN VARIOUS MISSISSIPPI DELTA AREAS DURING LATER FIELD TRIPS

	Field Trip		
	November 1956	*February 1957*	*May 1957*
Hourly production (μgm C/L/hour)	13.8	7.3	6.5
Estimated daily production (μgm C/L/day)	146	81	85
Number of determinations	2	16	1
Hourly production (μgm C/L/hour)	10.2	16.7	20.2
Estimated daily production (μgm C/L/day)	108	185	298
Number of determinations	9	21	9
Hourly production (μgm C/L/hour)	10.6	—	32.6
Estimated daily production (μgm C/L/day)	112	—	409
Number of determinations	6	0	25
Hourly production (μgm C/L/hour)	0.7	—	221
Estimated daily production (μgm C/L/day)	7	—	2,895
Number of determinations	1	0	1
Hourly production (μgm C/L/hour)	—	4.9	—
Estimated daily production (μgm C/L/day)	—	54	—
Number of determinations	0	2	0

MEAN AND MEDIAN CONCENTRATIONS OF SOLUBLE KJELDAHL NITROGEN (ORGANIC N PLUS AMMONIA) AT VARIOUS SEASONS IN VARIOUS AREAS OF THE DELTA

Area		*Fall Months*	*February*	*May*
River	Mean soluble N (μgm-atom/L)	3.93	5.02	4.78
	Median soluble N (μgm-atom/L)	3.93	5.60	4.78
	Number of determinations	2	4	2
Plume	Mean soluble N (μgm-atom/L)	2.88	3.20	5.30
	Median soluble N (μgm-atom/L)	1.14	1.96	6.36
	Number of determinations	14	12	4
Gulf	Mean soluble N (μgm-atom/L)	0.11	—	5.10
	Median soluble N (μgm-atom/L)	0.07	—	5.86
	Number of determinations	8	—	9
Breton Sound	Mean soluble N (μgm-atom/L)	2.20	2.28	1.78
	Median soluble N (μgm-atom/L)	0.50	2.28	1.78
	Number of determinations	5	1	2
Blind Bay	Mean soluble N (μgm-atom/L)	—	1.46	—
	Median soluble N (μgm-atom/L)	—	1.46	—
	Number of determinations	—	2	—

MEAN AND MEDIAN PHYTOPLANKTON CONCENTRATIONS AT VARIOUS SEASONS AND AREAS OF THE DELTA

	Fall Months	*February*	*May*
Mean phytoplankton concentration cells/ml	398	2,915	1,588
Median phytoplankton concentration cells/ml	111	3,056	1,588
Number of samples	3	4	2
Mean phytoplankton concentration cells/ml	237	1,988	1,078
Median phytoplankton concentration cells/ml	132	1,383	606
Number of samples	7	8	10
Mean phytoplankton concentration cells/ml	662	—	700
Median phytoplankton concentration cells/ml	316	—	572
Number of samples	8	—	26
Mean phytoplankton concentration cells/ml	1,619	22,097	3,202
Median phytoplankton concentration cells/ml	765	22,097	3,202
Number of samples	5	1	2
Mean phytoplankton concentration cells/ml	3,302	4,270	—
Median phytoplankton concentration cells/ml	3,795	3,264	—
Number of samples	4	3	—

Table 3. Photosynthetic productivities in the Missisippi delta Thomas and Simmons(1960).

SURFACE PRODUCTION AND ASSOCIATED MEASUREMENTS DURING SEAWARD TRAVERSES ON FEB. 21, 1957

Station Number	*Area*[1]	*Time*	*Hourly Production µgm C/L/Hour*	*Estimated Daily Production µgm C/L/Day*	*Secchi Disc Reading (cm)*	*Chlorinity ‰*	*Temperature °C.*	*Phosphate (µgm-atom/L)*
963	J	0735	14.2	158	10	0.12	14.0	0.91
964	J	0745	16.4	182	10	0.04	14.0	0.66
965	J	0805	21.2	235	10	0.04	14.2	1.05
966	K	0815	34.6	384	15	0.14	14.0	1.07
967	K	0840	18.8	209	100	5.69	16.0	2.31
968	K	0910	17.3	192	100	13.76	15.8	0.85
969	L	1230	25.2	280	76	14.91	14.5	0.90
970	L	1255	24.8	275	51	13.71	14.5	1.10
971	L	1310	21.6	240	76	12.26	16.0	1.23
972	L	1325	22.1	245	61	12.97	16.2	1.51
973	K	1400	16.2	180	8	0.14	16.2	1.16
974	J	1415	6.0	67	6	0.04	16.0	0.78
975	I	1445	1.7	19	6	0.04	14.0	0.90

SURFACE PRODUCTION AND ASSOCIATED PARAMETERS DURING SEAWARD TRAVERSES IN MAY 1957

Date	*Time*	*Station Number*	*Area*[1]	*Hourly Production µgm C/L/Hour*	*Estimated Daily Production µgm C/L/Day*	*Secchi Disc Reading (cm)*	*Chlorinity ‰*	*Temperature °C.*	*Phosphate (µgm-atom/L)*
1957 May 3	1445	988	A	6.5	85	3	0.06	19.4	0.35
	0750	984	C	3.6	47	20	2.43	20.1	2.67
	0830	985	E	7.3	96	107	8.64	22.2	0.57
	0915	986	F	24.0	314	244	14.08	24.5	0.43
	0945	987	F	28.9	379	315	15.11	23.9	0.43
May 7	0650	1,007	G	16.9	222	10	0.17	19.4	0.69
	0700	1,008	G	20.5	268	10	0.58	19.4	1.18
	0710	1,009	G	30.6	401	15	1.54	18.9	1.34
	0720	1,010	G	74.8	980	8	2.93	20.0	1.34
	0730	1,011	H	81.4	1,067	30	6.54	22.2	1.40
	0800	1,012	H	97.5	1,278	61	5.94	21.1	1.56

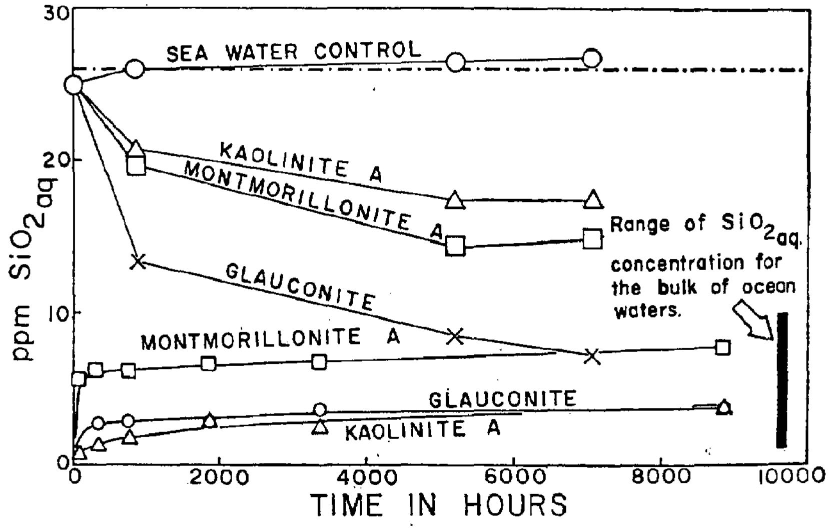
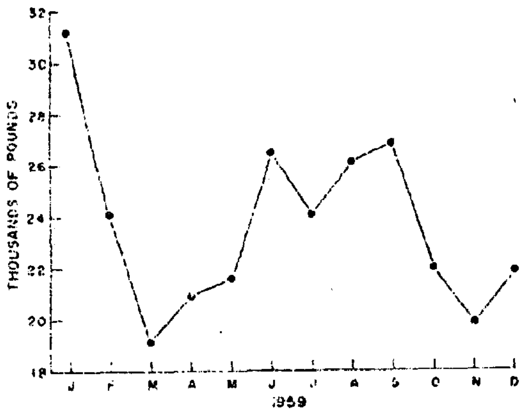
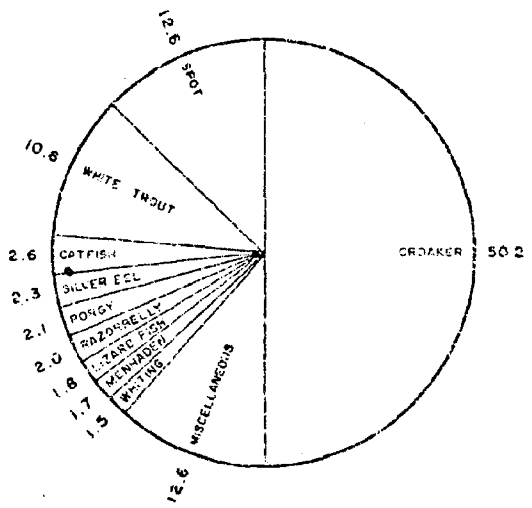


Fig. 1. Concentration of dissolved silica as a function of time for suspensions of silicate minerals in sea water. Curves are for 1-g ($< 62\ \mu$) mineral samples in 200 ml of silica-deficient (SiO_2 in water was initially 0.03 ppm) and silica-enriched (SiO_2 was initially 25 ppm) sea water at room temperature. Size of symbols indicates precision of SiO_2 determinations. Dash-dot line shows minimum SiO_2 concentration of sea water in equilibrium with a hydroxylated magnesium silicate at the *p*H's of our experiments.

Fig. 31 Control of silica content of waters by suspended clays (Mackenzie, Garrels, Bricker, Bickley, 1969).



Average monthly catch per trip of industrial fish by trawlers of four Mississippi petfood plants during 1959.



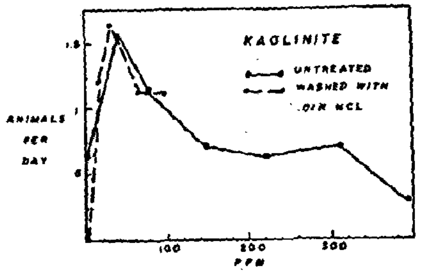
Species composition by weight of trawl-caught industrial fishes from January 1959 to April 1960.

Fig. 32. Trawl catch off the Missisippi River (Haskell, 1960).

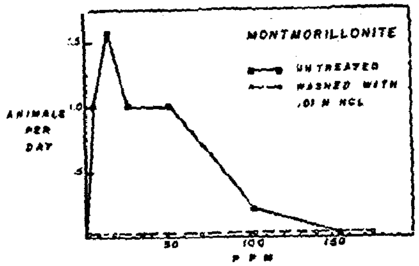
plankton as well. The number of zooplankton (tintinnids, copepods, worms, and larvae of various kinds) is about half the number of diatoms in any water sample. Similar distributions have been observed in front of many deltas, including the Mississippi. Robinson (1957) found suspended clays beneficial to filter feeding plankton (Fig. 33).

The fauna that inhabits the bottom can be divided into a microfauna, including foraminifera and ostrocods, and a megafauna that includes quite a variety of relatively large invertebrates such as clams, gastropods, and crustaceans. Within the active distributaries the bottom supports a unique foraminiferal fauna which is poor in number of species. The exact species vary with the actual salinity and temperature of the water, but they are types that are transitional between freshwater and marine varieties and capable of withstanding large salinity fluctuations. In the pro-delta slope area the fauna is adaptable to the rapid sedimentation rate. It consists of a few (usually three or four) species that have definitely marine affinities, and it is characterized by having a very large proportion of living population. This characteristic fauna has been studied in the Mississippi delta area by Lankford (1959), for example. When a delta builds into a lagoon or bay, where the salinity is not fully marine, the foraminiferal fauna may not have marine affinities, but it retains the characteristic that it is composed of a very high proportion of living forms of only three or four species. Beyond the pro-delta slope the species composition becomes more diverse. The temperature, water depth, and other ecological factors control species composition. Other small organisms, such as ostracods, show similar distributional characteristics between distributary, pro-delta slope, and bottomset plain regions.

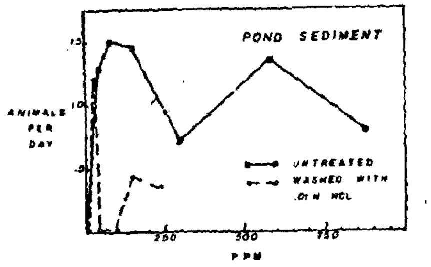
Distributions of the larger invertebrates are influenced by many of the same factors as discussed above. However, adjacent to the deltaic distributaries extreme fluctuations in salinity and water temperature, as well as an unstable substrate, produce environments that are extremely hostile to most larger, relatively immobile, invertebrates. The number of species that can populate such environments, therefore, is small. Within the distributaries, salinities become quite low during most stages of freshwater flow. This excludes marine pelecypods and similar sessile forms. The high turbulence and turbidity are other factors inimical to the existence of marine species. But the more motile animals--crabs, fish, shrimp, etc.--invade the distributaries when high salinity water enters them at periods of low freshwater flow. Should floods follow a period of extended drought, mass mortalities of the larger invertebrates are likely to occur. Adjacent to the distributaries where salinities are less than 10 o/oo, the faunas consist almost exclusively of a few pelecypods, a gastropod or two, two or three crustaceans, and a few fish of various sorts. Of these, the pelecypods are the largest and most diverse forms. They consist of four or five species (often including oysters). In the pro-delta slope region pelecypods, gastropods, and crustaceans become more abundant and diverse. The species become more akin to marine forms. The organisms are adapted to life on muddy bottoms and salinities just slightly less than marine. Beyond the pro-delta slope it is the nature of the bottom lithology--whether sand or mud--that is the dominant control of the faunal composition. Sandy bottoms sustain a very diverse group of marine pelecypods (a dozen species), gastropods (6-8 species), and occasionally echinoderms. Relatively few species occur on mud bottoms, but where found they are very abundant. As the water depth increases and siltation decreases farther away from the delta, species diversity increases and the number of known species becomes very large.



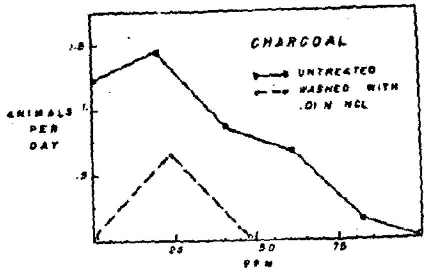
1. Reproductive Rate of *Daphnia magna* in Kaolinite. Kaolinite was shown to be non-toxic in levels as high as 392 ppm and to have a peak reproductive rate at 39 ppm. Kaolinite is comparatively unadsorptive and for that reason is apparently *not* deleterious to *D. magna*. A gradual tapering off of survival and reproduction is noted at higher concentrations. Broken line indicates that washed kaolinite was not more toxic than untreated kaolinite.



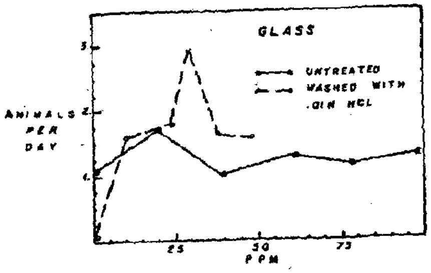
2. Reproductive Rate of *Daphnia magna* in Montmorillonite. Montmorillonite was toxic at levels greater than 102 ppm and had a peak reproduction at 13 ppm. This clay mineral is very adsorptive and this property appears to make it toxic to the plankter, *D. magna*. Broken line indicates the increased toxicity in acid washed montmorillonite. No animals survived at any of the levels tested in washed montmorillonite.



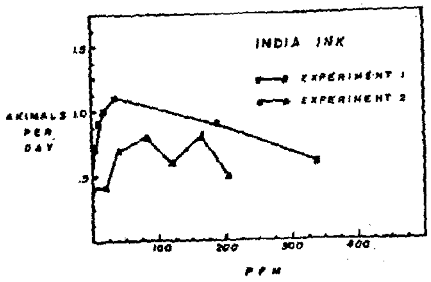
3. Reproductive Rate of *Daphnia magna* in Pond Sediment. Pond sediment was not toxic at levels up to 1458 ppm (concentrations as high as 874 shown in Fig. 8) and showed a peak in the reproduction at 73 ppm. Pond sediment was shown to contain kaolinite, vermiculite, illite and quartz. Dotted line indicates an increase in toxicity due to acid washing.



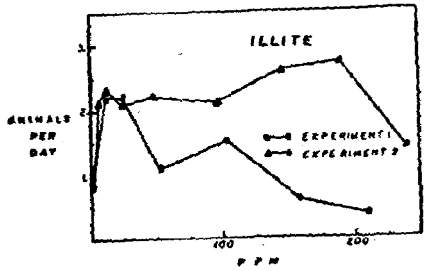
4. Reproductive Rate of *Daphnia magna* in Charcoal. Charcoal was toxic at levels greater than 82 ppm and had a peak reproduction at 20 ppm. This material is very adsorptive and apparently this property makes it very toxic to the plankter.



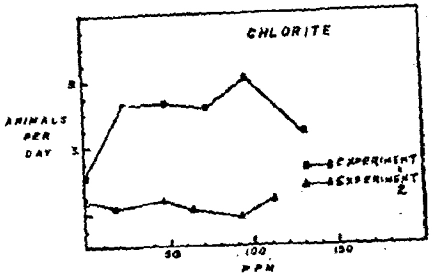
5. Reproductive Rate of *Daphnia magna* in Glass. Glass was tested at levels up to 98 ppm and was not found to be toxic at these concentrations. The peak reproduction was recorded at 20 ppm.



6. Reproductive Rate of *Daphnia magna* in India Ink. India ink was tested at levels up to 676 ppm and not found to be toxic. The highest reproduction was recorded at 34 ppm.



7. Reproductive Rate of *Daphnia magna* in Illite. Illite was tested at concentrations as high as 264 ppm and not found to be toxic. The high in reproduction was recorded at 26 and 192 ppm in the first and second experiments respectively.



8. Reproductive Rate of *Daphnia magna* in Chlorite. Chlorite was tested at levels as high as 120 ppm. In the first experiment the peak reproduction was recorded at 96 ppm. However, in the second experiment the controls were higher than the dilute suspensions, a condition which was not encountered in any other material.

Fig. 33. Effects of suspended materials on reproductive rate of a plankton species which was passing the materials through its gut (Robinson, 1957).

In Fig. 32 are data on the fish catch by trawlers operating in and around the delta system of the Mississippi; it gives some suggestion as to the fish populations.

The contrast between the delta and less disturbed surroundings is especially sharp in the work of Lowman and associates on the Añasco River example (Figs 19-30). Note the sharp changes in trace element contents of the sediments and the role of organisms in controlling many elements. The establishing of frequency distributions which show high , skewed variability of trace elements in biological materials is one of the results of these studies.

From the above discussion we see that the stresses imparted to ecological niches in the sedimentary delta environment are extreme and of a variety of kinds. Both speciation and species diversity reflect the dominant physical nature of these environmental stresses and their variations from one place to another.

Chapter A-6

HYPERSALINE LAGOONS

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INTRODUCTION

In the arid coastal regions where evaporation exceeds freshwater input, shallow estuarine waters become hypersaline (salinity above about 40 gm/kg (ppt)). These "lagoons" are characterized by the marked lack of freshwater input and they are isolated from the sea by long narrow barrier bars - their only connection with the sea is through "passes" in the narrow, often intermittent, barriers. As illustrated in Fig. 1 and in Fig. 2, the typical hypersaline lagoon tends to evolve parallel to the shore with narrow passes usually near the ends of the water body.

While the single most dominating feature of hypersaline systems is that of salinity, other parameters are important in determining which of the three main types of biological components will develop - grass flats, plankton based systems, or blue-green algal mats. When water depths are very shallow, perhaps 10 cm. or less, eddy diffusion becomes minimal and a laminar system may develop in which blue-green algal mats dominate and dissolved oxygen levels fluctuate widely between supersaturation during the day and anaerobic conditions at night (Sollins 1969). In deeper waters of several meters, where light may still penetrate to the bottom on calm days and salinity is not excessive, extensive underwater meadows of sea grasses may develop and serve as shelter and breeding grounds for fish and various invertebrates. Such grass systems may persist only where the morphology of the lagoon is such that the fetch of prevailing winds remains relatively small and turbid conditions do not result from wind generated waves churning up the shallow bottom. When the turbidity of the water becomes too great, plankton systems dominate over the light limited benthic ones and cause concomitant changes in the density and species composition of animal populations.

The concentration of salts in the hypersaline lagoon waters represent a sea to land concentration gradient, with the highest concentration being inland. With no head from river inflow to provide the circulation balance in the lagoon between fresh and sea water, there is a net inflow of sea water to replace the evaporation of water. This results in a net evaporation increase at the inland edge of the lagoon (or, in some cases, as distance away from the seawater source increases). With continued lack of freshwater input, the evaporation-seawater replacement phenomenon results in continued increase in general salinity of the water, such as has been the case in the Texas and Mexican lagoons during prolonged droughts.

On the landward side of hypersaline lagoons are the expansive areas known as pans and flats (see the illustration from Nichols 1966 as reproduced in Fig. 3). These shallow flat areas are important for nutrient circulation and

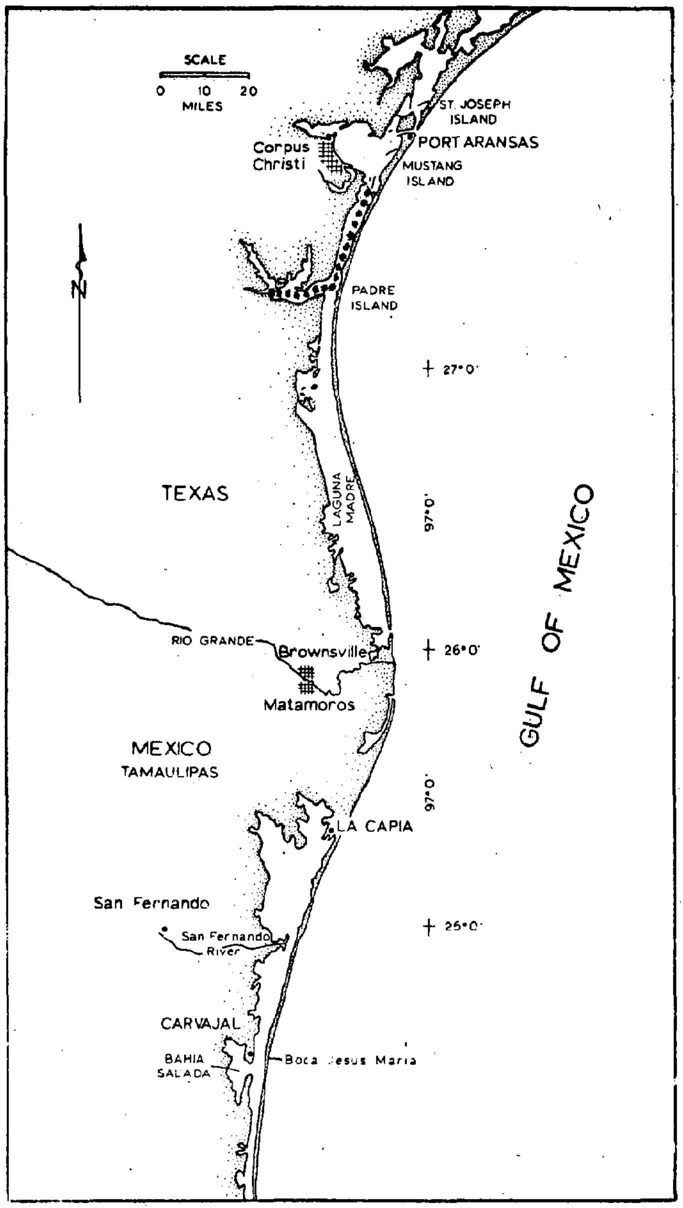

SCALE
0 10 20
MILES
N
ST. JOSEPH ISLAND
PORT ARANSAS
Corpus Christi
MUSTANG ISLAND
PADRE ISLAND
27°0'
TEXAS
LAGUNA MADRE
97°0'
GULF OF MEXICO
RIO GRANDE
Brownsville
26°0'
Matamoros
MEXICO
TAMAULIPAS
97°0'
LA CAPIA
San Fernando
San Fernando River
25°0'
CARVAJAL
BAHIA SALADA
Boca Jesus Maria

Fig. 1. Diagram illustrating the geographical location of the Laguna Madres of Texas and Mexico (From Copeland and Jones 1965; Fig. 1).

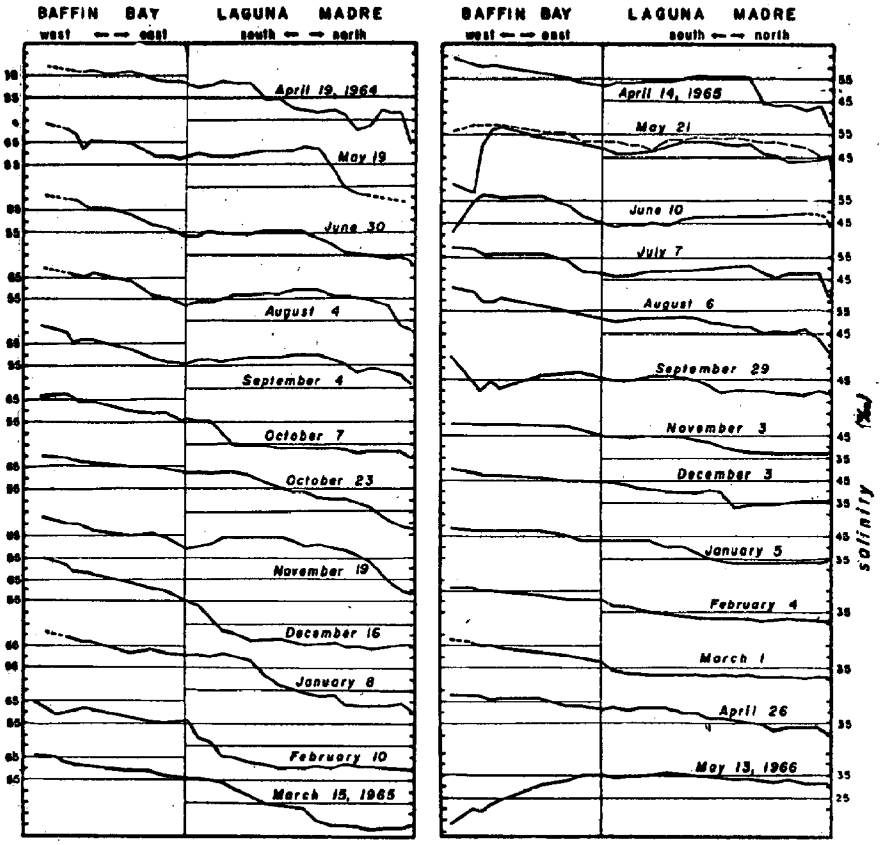


Fig. 2. Surface salinities for Baffin Bay and Laguna Madre, Texas (From Behrens 1966; Fig.2). The Baffin Bay-Laguna Madre sampling transect is indicated in Fig.1 by the dotted line.

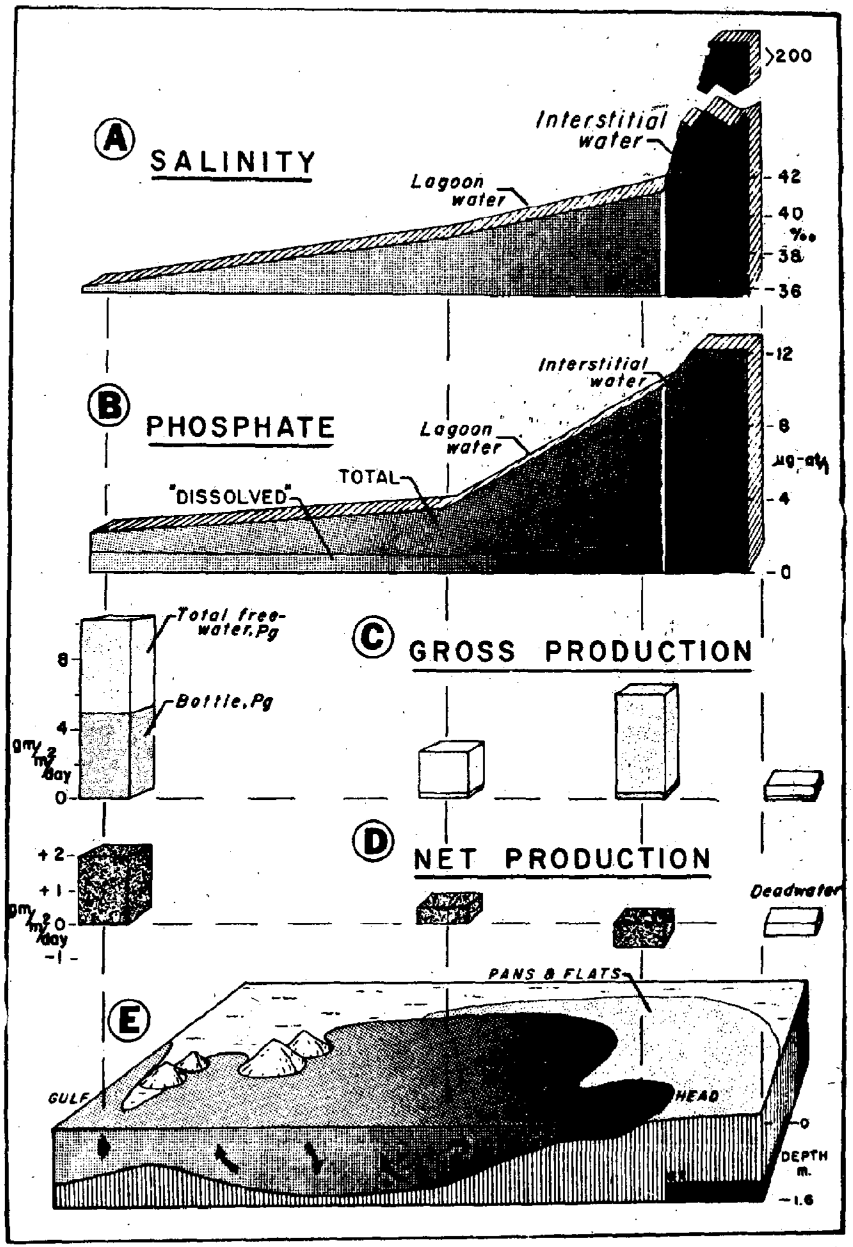

Ⓐ SALINITY
Interstitial water
Lagoon water
>200
42
40
‰
38
36
Ⓑ PHOSPHATE
Interstitial water
Lagoon water
TOTAL
"DISSOLVED"
12
8
µg-at/l
4
0
Total free-water, Pg
Bottle, Pg
8
4
0
gm/m²/day
Ⓒ GROSS PRODUCTION
Ⓓ NET PRODUCTION
+2
+1
0
-1
gm/m²/day
Deadwater
PANS & FLATS
Ⓔ
GULF
HEAD
0
DEPTH m.
-1.6

Fig. 3 . Horizontal distribution of salinity, phosphate, and community production in the hypersaline lagoon (Estero Tastiota) of Sonora, Mexico. From Nichols (1966).

net transport of water. The shallowness of the flat areas allows the rapid evaporation of water and generates a pattern of landward circulation. With the ebb and flow of waters due to wind changes and tidal effects, the flats are alternately drained and flooded. According to Nichols (1966), characteristic biogeochemical cycling in these areas results in a buildup of nutrient materials, such as phosphorous, in the evaporating pan waters, which are returned to the lagoon during the draining of waters from the flat.

Any biotic system that is capable of living in hypersaline waters must have the adaptive ability to contend with high salinity (osmotic problems), differential ion precipitation, and strange pH, dissolved oxygen and temperature regimes (Copeland 1967b). The results of this harsh environment are a reduced species diversity, a modification of biogeochemical cycles, a modification of the food web and a modification of the general productivity and economic value.

The contributive energies normally coming from river input with its organic and inorganic foods are almost completely eliminated in the hypersaline lagoon system, except during rare floods. The process of evaporation, however, tends to concentrate the inorganic and organic constituents of the water while decreasing the relative volume of water. The river input materials are also partially represented by the erratic floodwater contents from the arid drainage area (the infrequent rains in arid areas tend to come at irregular intervals and in large amounts, thus providing erratic input to the hypersaline lagoon).

EXAMPLES

Laguna Madre, Baffin Bay, of Texas

The Laguna Madre and Baffin Bay, Texas (Fig. 1) constitute the most extensive hypersaline lagoon system in the United States. Certainly it is the most intensively studied of such systems, and from the work of Collier and Hedgpeth (1950), Breuer (1957, 1962), Odum and Wilson (1962), Hellier (1962), Parker (1959) and Odum (1967b), a general composite diagram of the system can be made as in Fig. 4. The high solar insolation (greater than 700 gm.-cal./cm^2/day in summer, personal observation) generates substantial evaporation rates and results in natural stresses of high temperatures and salinities, especially in the shallower waters around the edges of the lagoon. As shown in Figure 4, these areas are dominated by extensive blue-green algal mats and associated bacteria. As salinities become increasingly higher as in the isolated arms of Baffin Bay (see Fig 4), less soluble salts such as $CaCO_3$ may become saturated and precipitate over the mat giving rise to oolitic formations characteristic of such environments. As evaporation continues, nutrients and organic materials are concentrated as well as salts, and this evaporative fertilization may be an integral part of the mechanism by which organisms are able to generate the energy necessary to meet the drains of osmotic stress adaptation. The concentrations of a major nutrient, phosphorus, in the Laguna Madre - Baffin Bay system are compared with those in the parent water of the Gulf of Mexico in Table 1.

As illustrated in Figure 2, there is a significant increase in salinity with increase in distance from the sea-lagoon connection. Behrens (1966) was able to show a 15 to 40 ppt. difference in salinity between the north end (lower)

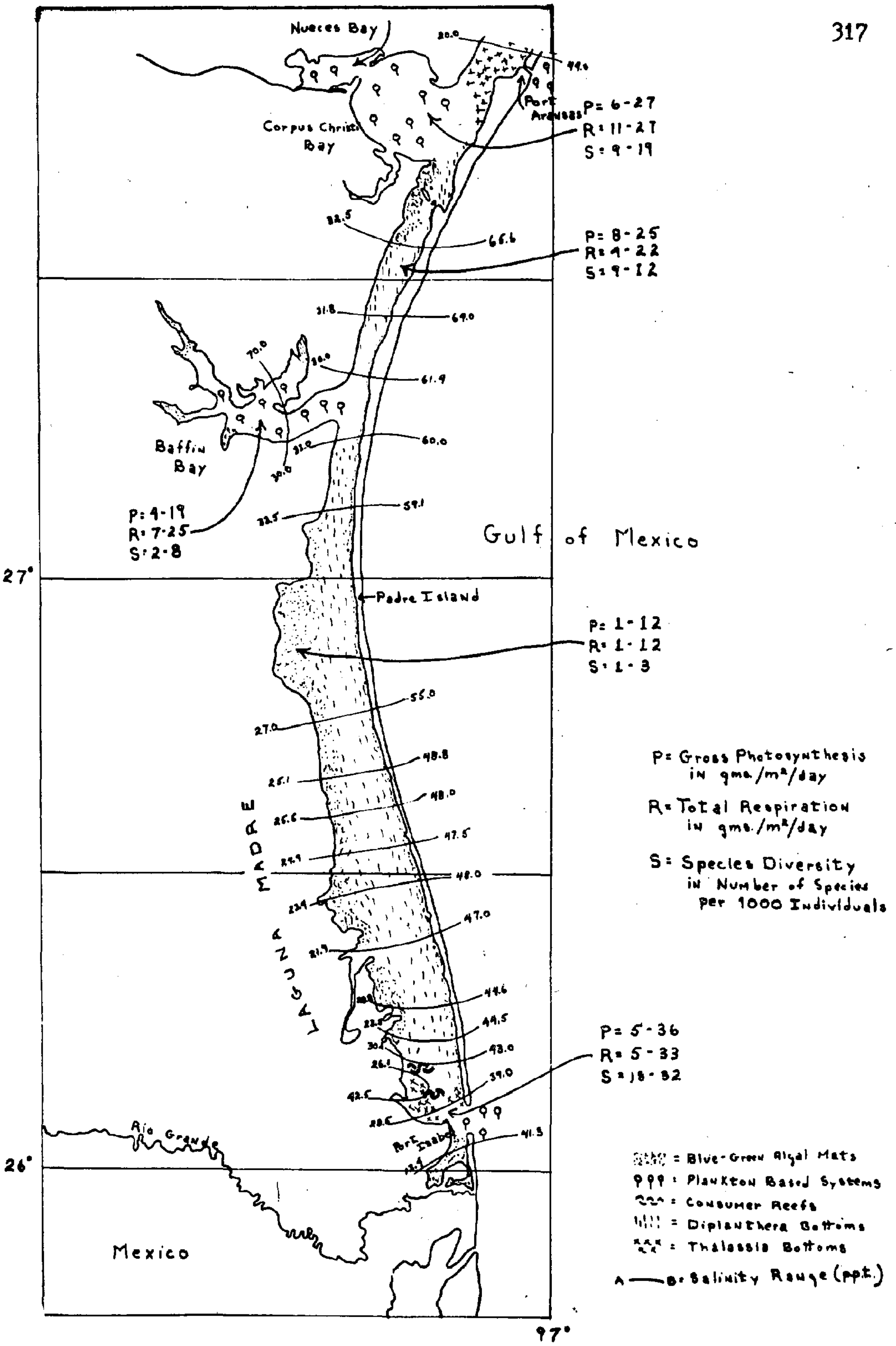

Nueces Bay
Corpus Christi Bay
Port Aransas
P= 6-27
R= 11-27
S= 9-19
66.6
P= 8-25
R= 9-22
S= 9-12
69.0
61.9
60.0
59.1
Baffin Bay
P: 4-19
R: 7-25
S: 2-8
Gulf of Mexico
27°
Padre Island
P: 1-12
R: 1-12
S: 1-3
27.0
55.0
48.8
48.0
47.5
48.0
47.0
44.6
44.5
43.0
39.0
41.5
LAGUNA MADRE
P= 5-36
R= 5-33
S= 18-32
Rio Grande
Port Isabel
26°
Mexico
97°
P= Gross Photosynthesis in gms./m²/day
R= Total Respiration in gms./m²/day
S= Species Diversity in Number of Species per 1000 Individuals
= Blue-Green Algal Mats
= Plankton Based Systems
= Consumer Reefs
= Diplanthera Bottoms
= Thalassia Bottoms
A——B= Salinity Range (ppt.)

Fig. 4. Composite diagram of the Texas Laguna Madre and Baffin Bay, showing the distribution of salinity in ppt, photosynthesis, community respiration, species diversity, and dominant communities (From Breuer 1962, 1957; Odum and Wilson 1962 and Odum 1967 b).

Table 1. Phosphorus concentration in mg-at/m^3 for Baffin Bay, Laguna Madre and Gulf of Mexico (From Odum and Wilson 1962; Table 2).

	Number of samples	mg-atom/m^3
HYPERSALINE BAYS, salinity, 50 to 70‰		
Baffin Bay, July 26, 1957	8	2.7–5.2
Baffin Bay, August 15, 1957	9	3.4–4.2
Upper Laguna Madre, July 23, 1957	4	1.4–3.2
Upper Laguna Madre, August 1, 1957	8	3.4–4.2
GULF OF MEXICO, salinity, 33 to 36‰		
Port Aransas jetties, July 15, 1957	8	2.0–2.2
Port Aransas jetties, July 23, 1957	1	1.8
Whistling buoy, Port Aransas, August 10, 1959	4	0.0–1.27

Table 2. Organisms normally found in Baffin Bay, Texas (with the exception of nannoplankton) (From Breuer 1957).

DIATOMS
- *Navicula* sp.
- *Amphiprora paludosa*

DINOFLAGELLATES
- *Ceratium hirundinella*

COELENTERATA
- *Phortis* sp.

CTENOPHORA
- *Beroe ovata*

MOLLUSCA
- *Mulinia lateralis*

COPEPODA
- *Acartia tonsa*

CIRRIPIDIA
- *Balanus eburneus*

AMPHIPODA
- *Gammarus mucronatus*

DECAPODA
- *Penaeus aztecus*
- *Callinectes sapidus*

FISH

Arridae
- *Galeichthys felis*

Cyprinodontidae
- *Cyprinodon variegatus*

Antherinidae
- *Menidia beryllina peninsulae*

Mugilidae
- *Mugil cephalus*

Sparidae
- *Lagodon rhomboides*

Sciaenidae
- *Cynoscion nebulosius*
- *Sciaenops ocellatus*
- *Micropogon undulatus*
- *Pogonias cromis*

Bothidae
- *Paralichthys lethostigma*

Table 3. Fishes normally caught in hypersaline areas in the Texas Laguna Madre and Baffin Bay (From Gunter 1967b; Table 1).

Laguna Madre To salinity 75 ppt	Baffin Bay Includes some species found only to 50-60 ppt
Elops saurus	*Galeichthys felis*
Anchoa hepsetus	*Cyprinodon variegatus*
Fundulus similis	*Menidia beryllina*
Cyprinodon variegatus	*Mugil cephalus*
Menidia beryllina	*Lagodon rhomboides*
Mugil cephalus	*Cynoscion nebulosus*
Lagodon rhomboides	*Sciaenops ocellatus*
Cynoscion nebulosus	*Micropogon undulatus*
Pogonias cromis	*Pogonias cromis*
Micropogon undulatus	*Paralichthys lethostigma*

of the Texas Laguna Madre and the west end (higher) of Baffin Bay (a distance of 40 miles), except during the infrequent times of heavy rainfall (May-June 1965 and May 1966). Other examples of salinity increase toward the inner areas of hypersaline lagoons include Breuer (1962) for the lower Texas Laguna Madre, Simmons (1957) and Collier and Hedgpeth (1950) for the upper Texas Laguna Madre, Nichols (1966) for a Sonoran lagoon, and Hildebrand (1958) and Copeland and Jones (1965) for the Mexican Laguna Madre.

Organisms

Due to the need for osmotic stress adaptation, the diversity of organisms in hypersaline waters is low (Copeland 1967b). The magnitude of the stress involved is a function of the energy drains of adaptive work required for the species to remain as a part of the particular system (Odum 1967b). Such energy demands are complicated and extended by fluctuations in the stress itself as pointed out by Parker (1959) in reference to the invertebrate animals of hypersaline areas:

> Both in hypersaline and very low-salinity regions, the variability and adversity of the environment determine the species composition and comparative abundance of each species. In extremely variable hypersaline areas, the number of species is very low, and the number of living individuals is small also. In stable hypersaline areas (and stable, very low-salinity waters), the number of species is still small, but the number of living individuals is extremely large. As the salinity decreases or increases to normal values (along with relative stability), the number of species increases and the number of individuals per species decreases.

Work by Breuer (1957) and by Gunter (1967b) among many others has affirmed the validity of this principle with respect to a variety of organisms living in the Laguna Madre-Baffin Bay complex, especially with respect to the fish of these environments. Their data are reproduced in Tables 2 and 3 respectively. Fish in the plankton based system of Baffin Bay tend to be largely planktivores, since the low productivity and the energy drains of osmotic stress may prohibit the development of an extensive level of secondary carnivorous consumers. This situation has been carried to the extreme in areas of brine pollution (see chapter on Brine Pollution Systems) where the fish population may consist entirely of planktivores. An idealized and simplified food web for Baffin Bay is shown in Fig. 5. It is unfortunate that little, if anything, is yet known of the bacteria and fungi of these systems, though there exist many species of decomposers that are capable of activity in even more severely stressed environments. Adequate substrates should be present in abundance in the form of vast acres of dead sea grass during the winter in the Laguna Madre, in the form of complex bacterial-blue-green algal mats across the extensive mud flats around the Laguna Madre and in the upper arms of Baffin Bay, and on the turbid particles of sediment suspended in the high levels of dissolved organics found by Wilson (1963) in the Baffin Bay area (see Fig. 6). It is interesting to note that Wilson was able to show some of the highest levels of dissolved organics associated with salinity stress in these systems and in the commercial salina systems of Puerto Rico. From his data, and those of others, Odum (1967b) was able to show an inverse hyperbolic relationship between species diversity and dissolved organic storage

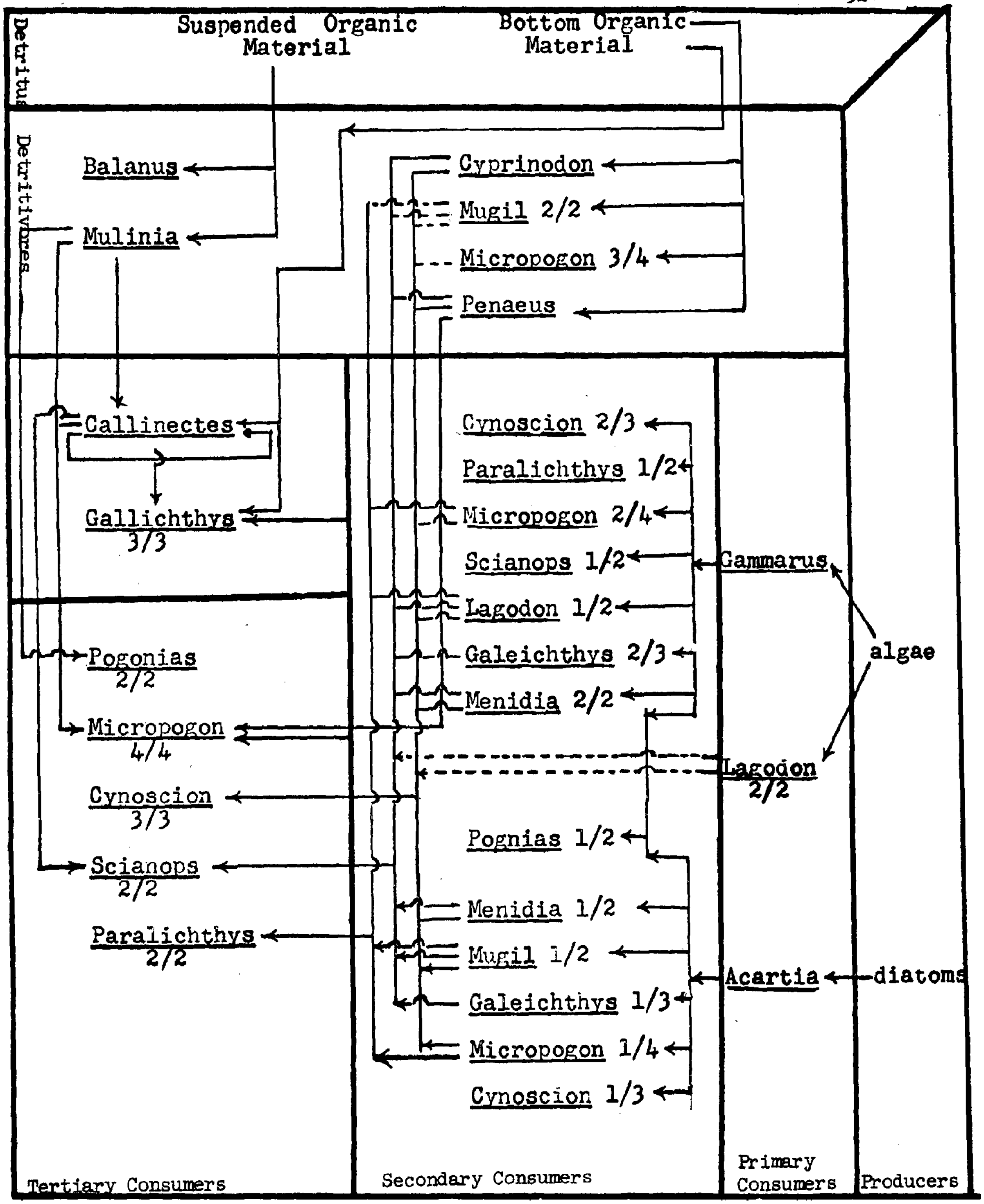

Detritus
Suspended Organic Material
Bottom Organic Material
Detritivores
Balanus
Mulinia
Cyprinodon
Mugil 2/2
Micropogon 3/4
Penaeus
Callinectes
Gallichthys 3/3
Cynoscion 2/3
Paralichthys 1/2
Micropogon 2/4
Scianops 1/2
Lagodon 1/2
Galeichthys 2/3
Menidia 2/2
Gammarus
algae
Pogonias 2/2
Micropogon 4/4
Cynoscion 3/3
Scianops 2/2
Paralichthys 2/2
Lagodon 2/2
Pognias 1/2
Menidia 1/2
Mugil 1/2
Galeichthys 1/3
Micropogon 1/4
Cynoscion 1/3
Acartia
diatoms
Tertiary Consumers
Secondary Consumers
Primary Consumers
Producers

Fig. 5. Idealized food web for Baffin Bay, based on data from Breuer 1962 (From Shapiro 1968; Fig. 1).

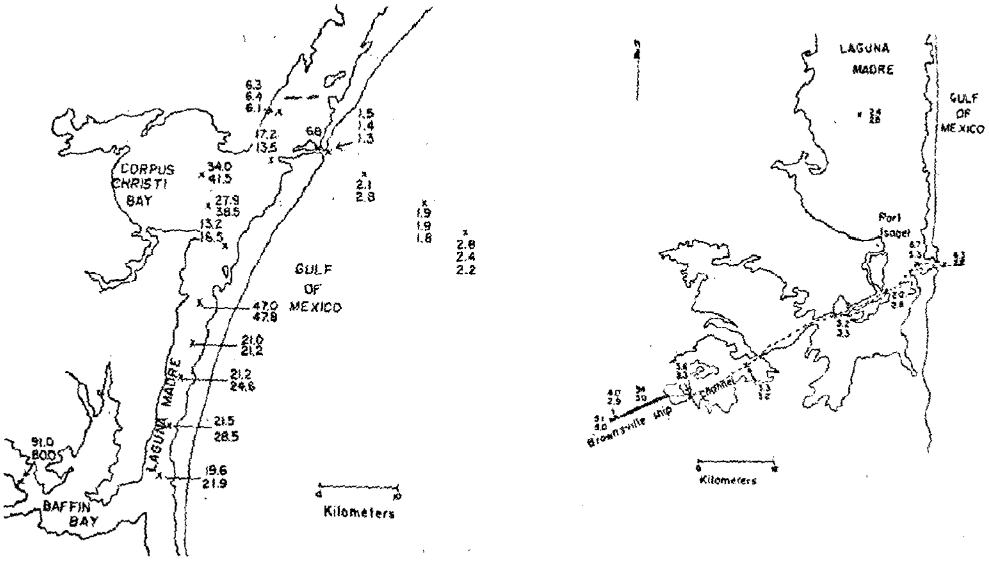

6.3
6.4
6.1
1.5
1.4
1.3
17.2
13.5
6.8
CORPUS CHRISTI BAY
34.0
41.5
27.9
38.5
13.2
16.5
2.1
2.8
1.9
1.9
1.8
2.8
2.4
2.2
GULF OF MEXICO
47.0
47.8
21.0
21.2
21.2
24.6
21.5
28.5
19.6
21.9
LAGUNA MADRE
91.0
800
BAFFIN BAY
Kilometers
LAGUNA MADRE
GULF OF MEXICO
Port Isabel
3.2
3.3
3.6
3.3
4.0
2.5
Brownsville ship channel
Kilometers

Fig. 6 . Total carbon in hypersaline waters of Baffin Bay and the Laguna Madre, Texas. Carbon in mg/l (From Wilson 1963; Figs. 3 and 4).

in the system. The possible significance of such large external storages has been discussed more fully in the chapter on Salina Systems and by Odum (1967b). In the Laguna Madre itself, where salinities are lower than in Baffin Bay and the water less turbid, the vast underwater grass beds of *Diplanthera* and, less significantly, *Thallassia* permit the development of more complex food webs based on the higher primary productivity of the benthic systems. The distribution, growth and reproduction of benthic algae and spermatophytes in the Laguna Madre have been described by Conover (1964).

As shown in Fig. 4, the prevailing winds of the "Texas" system are out of the southeast (U.S. Weather Bureau Records) so that the longest fetch is achieved across Baffin Bay and Corpus Christi Bay. These strong winds help to create very turbid water in the Baffin Bay system which shades out the benthic grass communities characteristic of the Laguna Madre and supports a low diversity system of plankton. In these systems production and biomass tend to be low compared with the grass systems, and respiration may exceed photosynthesis.

Metabolic patterns

Using the diurnal curve methods developed in Texas waters by Odum (1956) and Odum and Hoskin (1958), various investigators have obtained several years' data on the daily and seasonal changes in photosynthesis and respiration in the Laguna Madre - Baffin Bay complex, as well as biomass data for the important animal populations. Diurnal curves of oxygen in the Laguna Madre and Baffin Bay are given in Fig. 7. The depressed values for the Baffin Bay are partly the result of the decreasing solubility of oxygen in waters of higher salinity (Copeland 1967b), but the actual productivity of the system is indicated by the lower rate-of-change graphs where the values have been corrected for diffusion. The stippled area above the dashed zero line indicates net production occurring, while similar area below the line is a measure of system respiration. In systems where the area below the line is greater, as in Baffin Bay, respiration is exceeding photosynthesis and P/R ratios drop below 1.0. In the Laguna Madre, there is a greater area beneath the curve above the zero line, and there is a net production over 24 hours. Based on many such curves taken in all seasons and over a number of years, Odum and Wilson (1962) prepared the seasonal metabolic pattern curves shown in Figs. 8 and 9, as well as the values shown in Fig. 4 (Odum 1967b) Data in Fig. 8 indicate that the Baffin Bay system remains heterotrophic at almost all times measured and must therefore depend on some organic imports, perhaps from the less stressed Laguna Madre (Fig. 9) which is relatively well balanced in terms of production and consumption over a four-year period. Respiration follows productivity and in both systems they are highest with the strong seasonal pulse of solar input. As salinity stress increases, it appears that the energy necessary to cope with it also becomes increasingly available. It would be interesting to speculate if the effects of increasing salinities in systems are greater at higher latitudes (examples: brine pollution and brine residue from the freezing of sea water) where the solar energy input of the system is not so large as in naturally occurring subtropical hypersaline systems.

Role of migration of fish and crustaceans

Contributing to the balanced coupling of production and consumption in the Laguna Madre system are the migrating populations of breeding fish and associated invertebrate animals that enter the system because of the protection and food

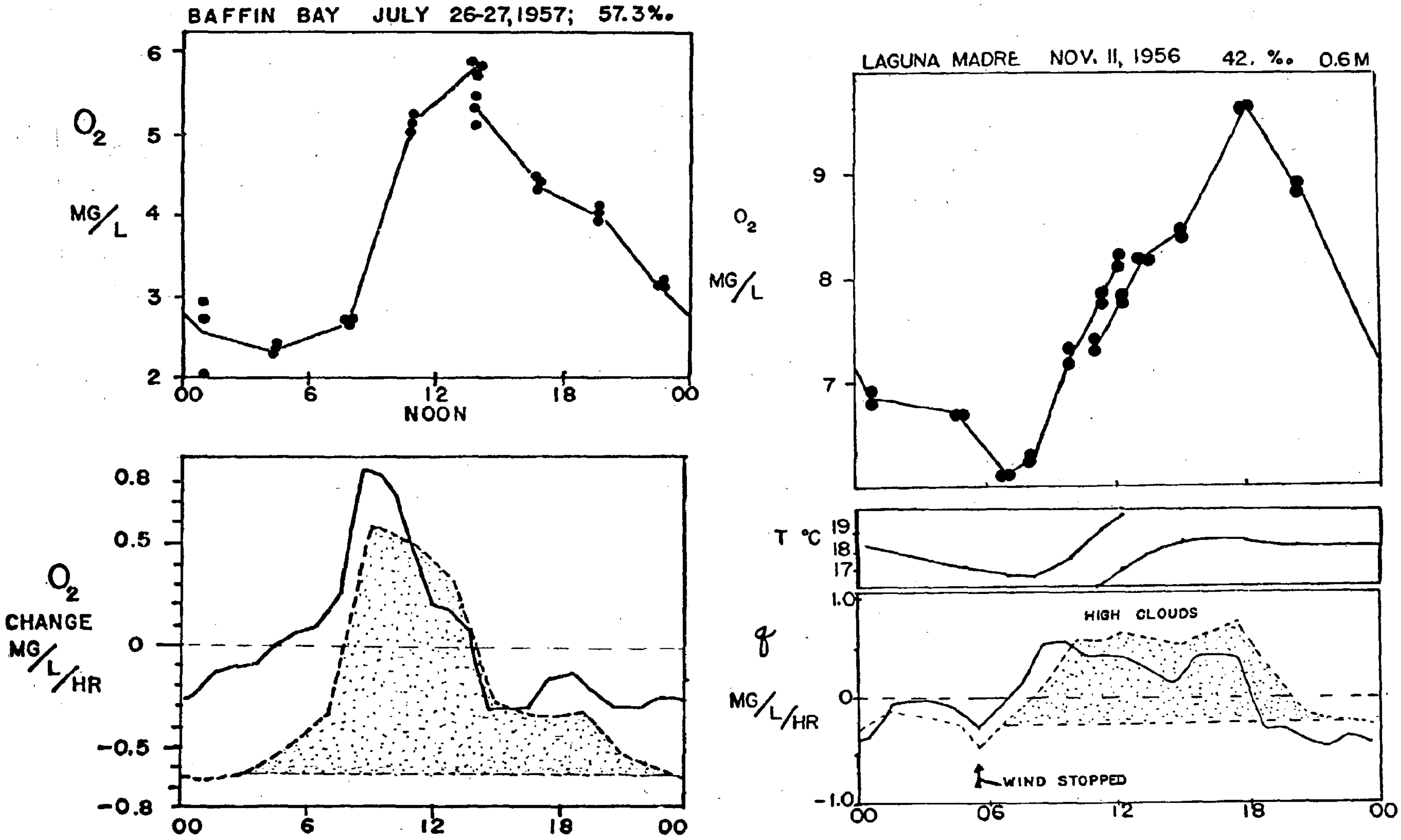


Fig. 7. 24 Hour data for dissolved oxygen and community metabolism in Baffin Bay (left) and Laguna Madre (right) (From Odum and Hoskin 1958; Figs. 4 and 6).

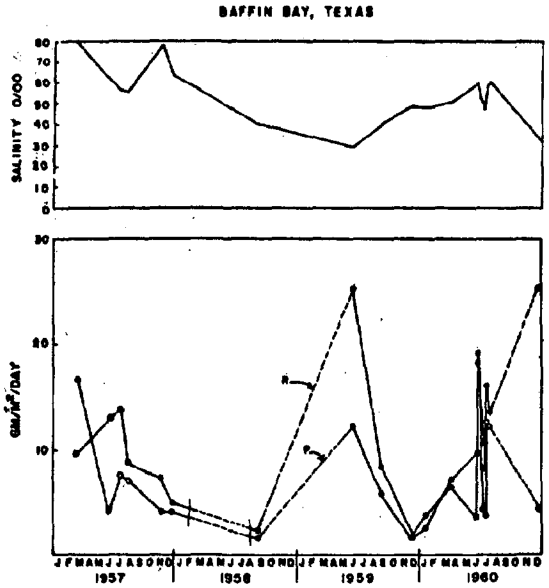


Fig. 8. Community metabolism data from Baffin Bay, Texas during 1957 through 1960 (From Odum and Wilson 1962; Fig. 24).

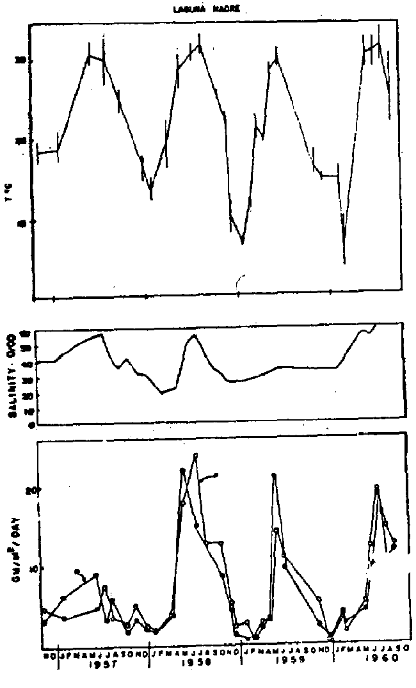


Fig. 9. Community metabolism data from the Laguna Madre during 1957 through 1960 (From Odum and Wilson 1962; Fig. 7).

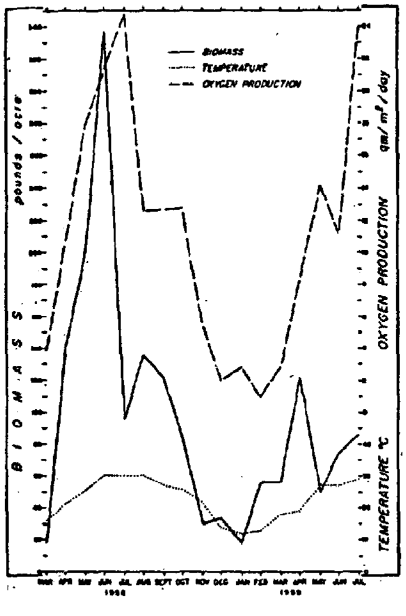


Fig. 10. Total biomass of animals from a drop-net quadrant compared with gross primary production in the Laguna Madre (From Hellier 1962; Fig. 13).

offered by the grass beds. Work by Hellier (1962) has shown a propensity for the animals to, in effect, arrive in the area just as the food becomes available. When the total animal biomass shown by Hellier in Fig. 10 is broken down into the individual component species, the same general trend remains (Hellier 1962).

Laguna Tamaulipas, Mexico

In northeastern Mexico south of the Texas Laguna Madre (Fig. 1) there is a similar long lagoon running parallel with the coast as part of the same geological continuum of offshore barrier islands and shallow water systems. Here, in the Mexican Laguna Madre (Laguna Tamaulipas), conditions were very similar to those of the Laguna Madre of Texas until 1961, when the narrow passes that served to connect the Laguna Tamaulipas with the Gulf of Mexico were filled in by hurricane generated waves and currents. Once these sources of sea water input were closed the continuing effects of evaporation became more pronounced and salinities rose to produce the only remaining coastal bay within or adjacent to the United States that resembles the primeval conditions which existed prior to the rise of extensive industrialization and civilization along the Texas coast. During the past few years, due to natural changes in the morphology of the lagoon and barrier island, the Laguna Tamaulipas has ranged in salinity from almost fresh to sodium chloride saturation (about 290 ppt) (Copeland and Jones 1965; Copeland 1967b, personal observation). This process of concentration produced new and far greater stresses resulting from differential ion precipitations and greatly reduced oxygen solubility, as well as pH fluctuations and extreme osmotic energy drains. Such a system also comes to resemble those of commercial salina systems where sea water is evaporated to produce salt, but with the important exception that the water is not removed from the salts as they precipitate. Studies of the changes in gross productivity, community respiration, and species diversity of fish were reported by Copeland and Jones (1965) and Copeland (1967b) as a function of increasing salinity over the five year period 1961-1965. Their results, as shown in Fig. 11, show the expected sharp decrease in fish diversity with increasing salt stress. Once again, their data make the point of increasing respiration with stress while gross productivity decreases. Unlike the salina, this system failed to develop great numbers of red halophilic bacteria at the highest salt levels, and as a consequence respiration appeared to drop at the final stages of succession.

Lagoons of lower California

Along the west coast of the United States undisturbed hypersaline lagoons once existed in parts of southern California. Further south, along the shore of the Gulf of California in Mexico, Nichols (1966) has studied the phosphate levels and metabolism of still unpolluted Sonoran lagoons. His results again point out the importance of wind in generating turbulence and turbidity which decrease production in shallow water systems. Phosphorus and salinity gradients are shown in Fig. 3 emphasizing a positive correlation that is similar to that in the Laguna Madre-Baffin Bay area (see Fig. 3) and results from progressive evaporation and, to some extent, from land inputs of phosphorus during brief erratic flooding. Fig. 3 also indicates that net production was lowest in the turbid grass (Zostera) system in the center of the lagoon and highest in the deeper, less turbid plankton system off the lagoon mouth. The surrounding pans and flats were dominated by

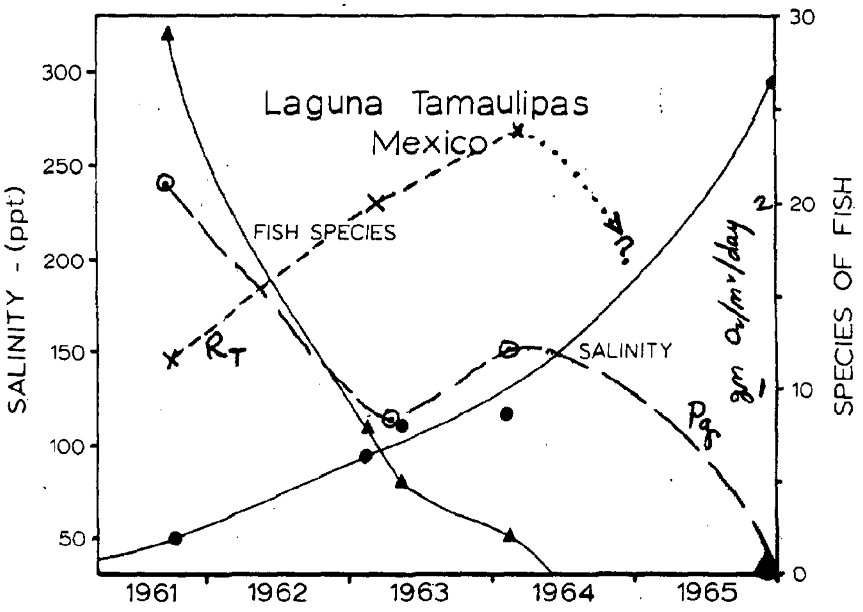
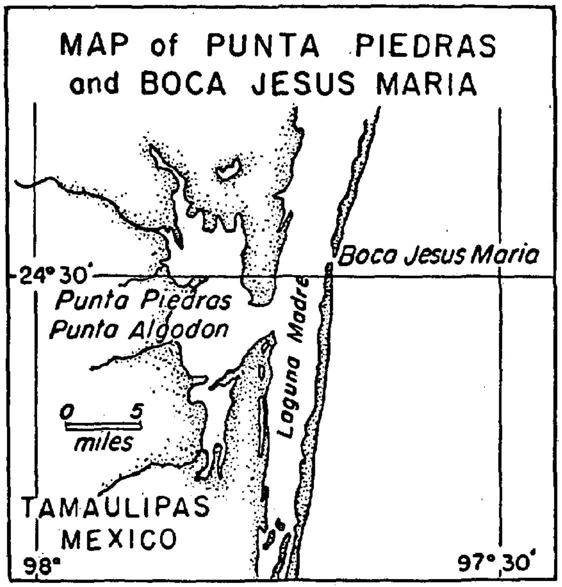


Fig. 11, Salinity, fish species, gross photosynthesis and community respiration for the Mexican Laguna Madre, 1961-1965 (From Copeland and Jones 1965; Copeland 1967b).


MAP of PUNTA PIEDRAS and BOCA JESUS MARIA
Boca Jesus Maria
24° 30'
Punta Piedras
Punta Algodon
Laguna Madre
0 5
miles
TAMAULIPAS
MEXICO
98°
97° 30'

. Areas from which collections were obtained in the lower Laguna Madre of Mexico near Boca Jesus Maria.
(Humm and Hildebrand, 1962)

blue-green algal mats having intermediate levels of net production. Except for the interstitial water of the pans and flats, however, salinities in this system were considerably lower than those in the Laguna Madre or Laguna Tamaulipas.

Hypersaline pool - St. Joseph Island, Texas

The high spring sea levels occurring along the Gulf Coast of Texas in April fill shallow depressions in the barrier islands with sea water. Through the following months, this trapped water evaporates and becomes increasingly hypersaline. By July, carbonate has begun to precipitate and the system is dominated by red and pink bacteria that may ultimately come to constitute a heterotrophic system based on energy fixed and stored by earlier, less stressed systems. Such ponds would provide an excellent system for the study of changes in species diversity and metabolism in a successional sequence that moves from low stress autotrophic to high stress heterotrophic. Copeland and Jones (1965) have obtained measurements of the oxygen and carbon dioxide metabolism in a hypersaline pool on St. Joseph Island in mid July, before the system has become completely dominated by pink bacteria. Their diurnal oxygen curve is shown in Fig. 12 and indicates a very wide range from anaerobic at night to over 250% saturation during the peak daylight hours. The ratio of gross photosynthesis to total respiration was 0.83 when computed from oxygen data and 2.27 when computed from carbon dioxide data. The R.Q. was 0.3. Such unusual metabolic behavior, perhaps related to the extensive bacterial components, may imply interesting ecological principles of stress adaptation in these isolated ephemeral systems.

DISTURBANCES

With biological communities already stressed in hypersaline systems, disturbances in the system may tend to cause the elimination of more species than similar disturbances in less stressed environments where energy reserves may be sufficient for adaptive work. With organisms living at the limit of their adaptive ability, they could be eliminated from the system with only small additional energy drains. Also, if some material that was toxic to even a single species was introduced into the hypersaline stressed system, a whole food chain could be eliminated because of the inherent simplicity of the community.

Impoundment

When the Mexican Laguna Madre was impounded due to the natural closing of its pass to the Gulf of Mexico in 1961, evaporation and sedimentation proceeded to lower the productivity (Copeland and Jones 1965). After about three years of evaporation without replenishing rainfall, the salinity in the system had reached the level found in salinas and the ecology of the system was similar. A diurnal oxygen curve (Fig. 13), as reported by Copeland and Jones (1965) for a station near Carvajal (See Fig. 1 for orientation), indicated that the diurnal oxygen flux was very low. The magnitude of oxygen concentration was also very low due to the increased salt concentration (Copeland 1967b) and fell below saturation values even during the daylight hours. The lower saturation indicated some oxygen demand and community stress.

Price (1968) studied the effects of impounding a 35,000 acre mudflat on the west side of the Texas Laguna Madre. The spoil from the construction of

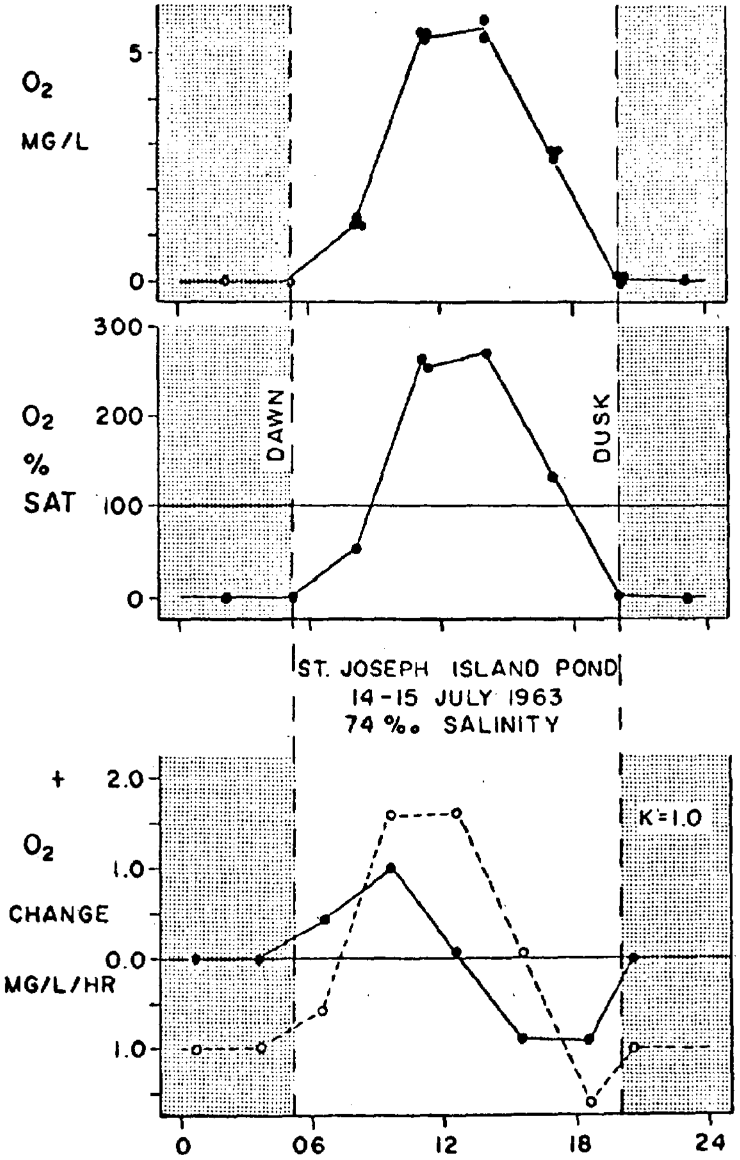


Fig. 12 . Diurnal oxygen curve for the St. Joseph Island Pond, Texas for 14-15 July 1963 (From Copeland and Jones 1965; Fig. 7).

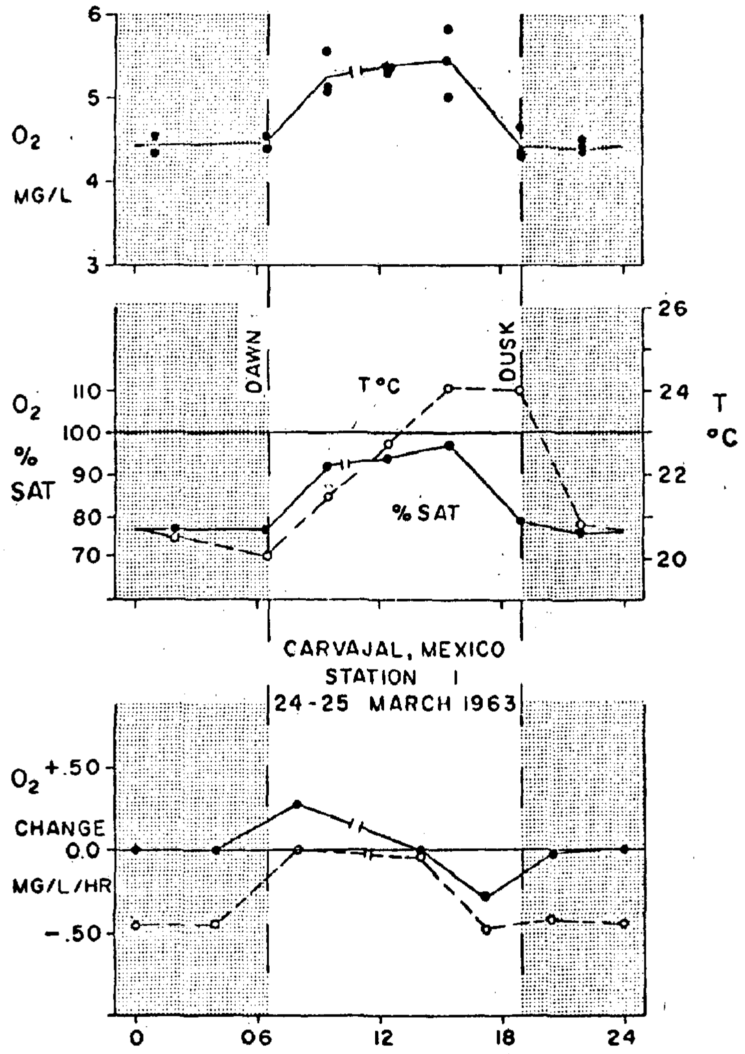


Fig. 13. Diurnal oxygen curve for station 1 at Carvajal in the Mexican Laguna Madre (From Copeland and Jones 1965; Fig. 5).

the intracoastal canal through the Laguna Madre was placed along the Laguna side of the extensive mudflat area. With the prevention of normal flushing of waters across the mudflat during wind shifts and high tides by the spoil dyke, the water over the mudflat (over a portion of the mudflat during extremely high spring tides) evaporated and the strong prevailing winds blew salt-laden sand westward over several thousand acres of pasture land and killed the grass. The extensive blue-green algal mat that had spread over the entire mudflat during the normal flushing and draining activities was destroyed, leaving exposed soil overlaid with salt crystals.

Organic Pollution

Sewage disposal at La Capia in the Mexican Laguna Madre (Copeland and Jones 1965), resulted in lowering the oxygen concentration to zero. The organic material in the presence of high salt concentrations settled to the bottom and smothered the dominant algal bottom community. This lowered the productivity and the species diversity of the system to almost zero.

Dredging Spoil

The deposition of dredging spoil in the upper Laguna Madre of Texas covered the grass beds and blue-green algal mats on the shallow flats, thereby eliminating the dominant bottom producers. With the shallowness of the water, extensive plankton systems could not develop because of the lack of circulation and flushing (Odum and Wilson 1962). The net result was a decrease in productivity of the covered area and elimination of fish species.

Navigation Channel

Hypersaline conditions over 100 p.p.t. existed naturally in the Texas Laguna Madre until 1949 when the completion of an intracoastal waterway modified the morphological characteristics that once existed. According to Collier and Hedgpeth (1950) and Behrens (1966), the establishment of extreme hypersaline conditions that were once possible has been prevented by the availability of larger volumes of water from Corpus Christi Bay on the north and the Gulf of Mexico on the south via the intracoastal canal. This is possible because the sills that existed at both ends of the Laguna Madre have been cut by the canal. A similar waterway is projected for the Mexican Laguna.

Chapter A-7

MARINE BLUE-GREEN ALGAL MATS

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Chapel Hill, North Carolina

INTRODUCTION

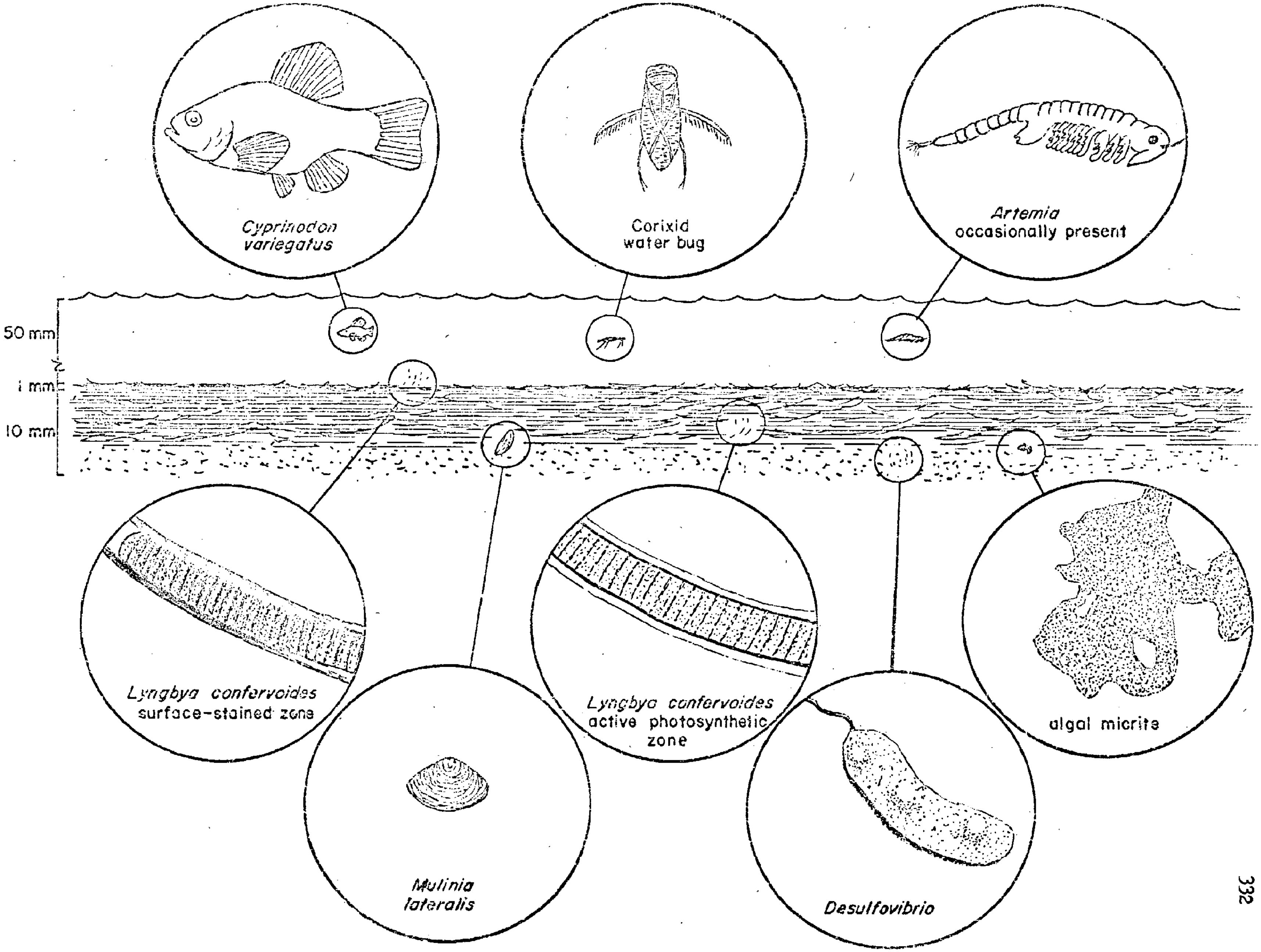
Very shallow coastal waters are often subject to extreme environmental stress. This stress may result from the high diurnal ranges of natural properties such as oxygen and temperature that are influenced by daily variations in the sun's insolation or by pollutants from the adjacent land. In these areas the varying or extreme conditions favor organisms highly adapted to this stress which are able to form viable ecological systems. Blue-green algae are especially well suited to this type of environment (Vinyard 1966) and grow abundantly under these conditions where ordinary floras and faunas cannot survive. Associated with the blue-green algae, is also a collection of plants and animals unique to this system, but the nature of the physical environment causes species diversity to remain normally quite low (Fig. 1).

EXAMPLE - MATS IN SHALLOWS OF SOUTH TEXAS

An example of a blue-green algal mat system is located on sandy shallows around Baffin and Alazan Bays and the Laguna Madre on the southern Gulf Coast of Texas (Fig. 2). The high evaporation, low precipitation and little fresh water input of this region (Diener,1964) frequently cause these bays to become hypersaline.

Adjacent to these shallow salty bays, vast areas of land are occasionally flooded, and as the water recedes some of it is trapped on the surrounding sand flats. In this thin layer of water the salinity varies from oligohaline to extremely hypersaline conditions and wide diurnal ranges of temperature, oxygen, redox and pH are present (Odum, Siler et al 1963).

Very few organisms are capable of adapting to this harsh environment, but the blue-green alga, Lyngbya confervoides, finds conditions favorable. In some areas this alga forms dense mats and often constitutes 80% of the living community (Sorenson and Conover 1962). Other blue-green algal genera, Oscillatoria, Microcoleus, Schizothrix, Phormidium and Anacystis are also present but not usually as abundant (Armstrong and Odum 1964; Odum 1967b). In addition, unicellular green algae, flagellates, diatoms, pink and purple bacteria are occasionally found (Sorenson and Conover 1962; Odum, Cuzon du Rest et al 1963). High concentrations of the bacteria Desulfovibrio and Beggiatoa have also been observed (Armstrong and Odum 1964).



Cyprinodon variegatus
Corixid water bug
Artemia occasionally present
50 mm
1 mm
10 mm
Lyngbya confervoides surface-stained zone
Mulinia lateralis
Lyngbya confervoides active photosynthetic zone
Desulfovibrio
algal micrite

Fig. 1. Representative blue-green algal mat and some associated biota.

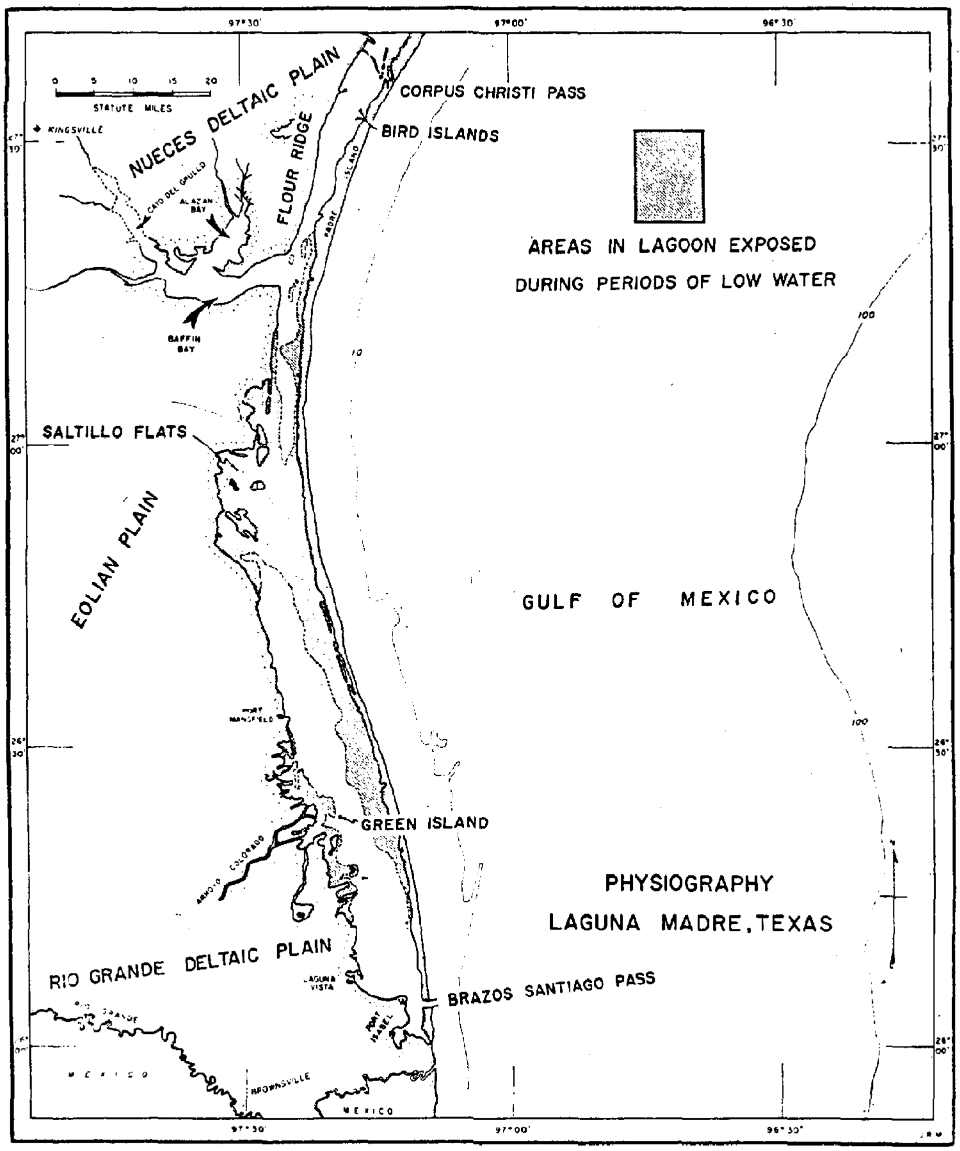

97°30'
97°00'
96°30'
0 5 10 15 20
STATUTE MILES
KINGSVILLE
NUECES DELTAIC PLAIN
FLOUR RIDGE
CAYO DEL GRULLO
ALAZAN BAY
PADRE ISLAND
CORPUS CHRISTI PASS
BIRD ISLANDS
AREAS IN LAGOON EXPOSED DURING PERIODS OF LOW WATER
BAFFIN BAY
10
100
27°30'
SALTILLO FLATS
27°00'
EOLIAN PLAIN
GULF OF MEXICO
PORT MANSFIELD
26°30'
GREEN ISLAND
ARROYO COLORADO
PHYSIOGRAPHY
LAGUNA MADRE, TEXAS
RIO GRANDE DELTAIC PLAIN
LAGUNA VISTA
BRAZOS SANTIAGO PASS
PORT ISABEL
RIO GRANDE
26°00'
MEXICO
BROWNSVILLE

Fig. 2. Map showing the shallow flats around the Laguna Madre, Baffin and Alazan Bays in South Texas. (Modified from Rusnak, 1960; Fig. 2)

The animal kingdom is limitedly represented by ciliates, nematodes, crustaceans, corixid water bugs, and an assemblage of worms (Sollins 1969). In the mud beneath the mat the small clams, Mulinia lateralis and Anomalocardia cuniemeris, are occasionally present (Dalrymple 1965); and in the waters above the mat Cyprinodon is frequently active in salinities as high as 120°/oo (Odum, 1967b). Davis (1966) describes waterbug reproduction in 43% salinity in saline waters of Jamaica.

DISTRIBUTION

Naturally occurring blue-green algal mats are found typically associated with warm water. Shallow coastal areas around the Gulf of Mexico often contain blue-green algal mats (Sorenson and Conover 1962) and the frequency of occurrence becomes greatest in the harsh, dry environment of South Texas. Along the East Coast of the United States as far north as New Jersey, mats can occasionally be found (Pomeroy 1959; B. J. Copeland, personal communication 1969). California, Hawaii, and Puerto Rico also have naturally occurring mat systems (See Chap. E-13).

In many other areas pollution may result in the production of blue-green algal mats. Chief among the stresses that result in mat formation is brine pollution from oil wells and salt producing industries. The Leslie Salt Co. of San Francisco, California, and the Ponce Salt Works in Puerto Rico have developed mat systems (See Chap. E-13 and E-14).

SYSTEM CHARACTERISTICS

Environmental Conditions

Blue-green algal mats are found in tidal basins, small depressions near the shore and broad lagoons which contain from 1 to 50 cm. of water (Sorenson and Conover 1962). The development of most mats occur, however, in water less than 10 cm. (Odum 1967b).

It has already been noted that most mats develop in warm waters. Algal cells can withstand annual temperatures from near freezing to 70°C (Sorenson and Conover 1962) but mats disintegrate in the winter with lowered temperatures (Pomeroy 1959; Odum, Siler, et al. 1963).

Alternate drying and wetting of the mats cause shrinkage and sloughing from the mud surface. When dried, patches of surface crust are often lost to high winds but this dehydration does not usually cause permanent injury. The addition of water to dried algal mat restores vigorous photosynthetic activity within a few hours (Sollins, 1969).

Wide ranges of salinity are associated with blue-green algal mats (1% to > 20% salt) but salt concentration apparently has little or no effect on the mat except at very low salinities (Sorenson and Conover, 1962).

Ginsburg et al (1954) further discusses the factors that influence mat growth and lists them as illumination, moisture, sediment (grain size), substrate (nutrients), and associated organic growth factors. Little work has been done, however, to determine the relative effect of each parameter.

Community Structure

Living mats consist of a laminar arrangement of living plants and animals. Each layer differs in color and composition. While mats from different geographic areas may be composed of different species they all exhibit a typical zonation of a darkly stained surface, lustrous blue-green center, yellow deep layers and a black bottom area (See Fig. 1).

A typical mat is composed of three major zones (Sollins 1969). The first is a felt-like photosynthetic zone consisting of closely packed filaments up to one centimeter thick. The second region is less consolidated and nutrition is largely heterotrophic. The third layer is highly anaerobic containing H_2S and reduced organic matter. This last layer may extend several feet downward where it gradually blends with the sandy soil.

Sorensen and Conover (1962) further divide the photosynthetic zone into three additional zones (Fig. 3). The first, or top, zone (A) is dark brown to black and acts primarily as a light and temperature shield. This color is due to the staining of Lyngbya sheaths. Staining produces a papery crust 1-20 mm deep. Originally it was thought that staining was due to a ferric colloidal complex (Correns,1889) but later investigations (Kylin, 1937) suggest that the staining is due to a photo-chemical process involving the pigment "scytonemine.' The staining apparently only takes place in direct sunlight and is very effective in reducing incident light (up to 95% lost within the first 0.5 - 1.0 mm).

Very little photosynthetic activity takes place in the first, stained zone. The second zone (B) of the mat produces some additive growth but only in the third zone (C) does photosynthesis reach a peak (See Fig. 3). Below Zone C the bacteria increase in number and light intensities above the compensation point are rare. The layered structure of the mat acts similar to other aquatic ecosystems, like the Black Sea, in having sharply defined oxidized epilimnetic and reduced hypolimnetic zones; but the extreme gradations are made over a much shorter distance (Armstrong and Odum 1964). Characteristics of the various zones as described by Sorensen and Conover (1962) are given in Table 1.

Chemical Environment

Evaporation of shallow water over blue-green mats may concentrate organic matter up to 100 mg/l (Wilson, 1963). The surface mat, composed of mucilaginous sheaths and intertwining filaments, trap or fix much of this material. Also, co-precipitation with inorganic salts build up high amounts of organic matter in the mat. The result is a distinctive grain type termed algal micrite. The Baffin Bay micrite is composed essentially of

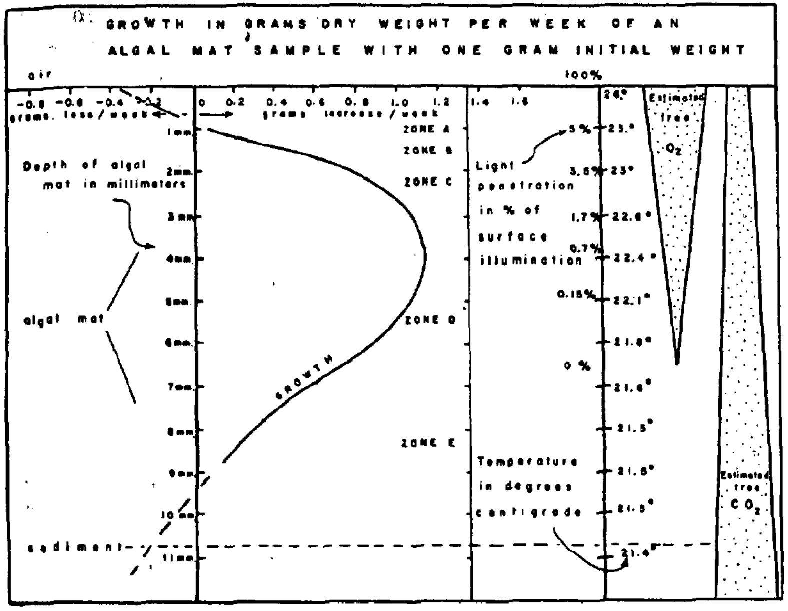
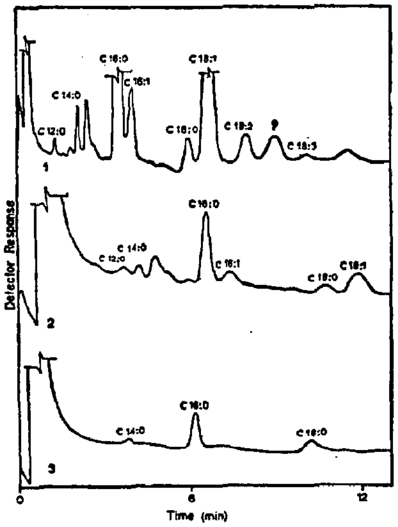

GROWTH IN GRAMS DRY WEIGHT PER WEEK OF AN
ALGAL MAT SAMPLE WITH ONE GRAM INITIAL WEIGHT
air
100%
-0.8 -0.6 -0.4 -0.2
grams. loss / week
0 0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6
grams increase / week
1mm.
2mm.
3mm.
4mm.
5mm.
6mm.
7mm.
8mm.
9mm.
10mm.
11mm.
Depth of algal mat in millimeters
algal mat
sediment
ZONE A
ZONE B
ZONE C
ZONE D
ZONE E
GROWTH
Light penetration in % of surface illumination
5%
3.5%
1.7%
0.7%
0.15%
0 %
Temperature in degrees centigrade
24°
23.°
23°
22.6°
22.4°
22.1°
21.8°
21.6°
21.5°
21.5°
21.5°
21.4°
Estimated free O_2
Estimated free CO_2

Fig. 3. Hypothesis of growth of Lyngbya confervoides for each zone within the mat profile. The growth curve also represents the general growth trend for the mat community since all mat organisms were contributing to the increase measured (Sorensen and Conover, 1962).



Gas chromatogram of methyl esters of fatty acids from algal mat: 1, the living mat; 2, first mud layer; 3, second mud layer.

Fig. 4. Characteristics of blue green mats. The second number indicates the number of double bonds in the fatty acid (Parker and Leo, 1965).

Table 1. Comparison of characteristics from natural blue-green mats and those grown in the laboratory in microcosms (Sorensen and Conover, 1962).

Characteristics of environment from which experimental material was obtained for experiments

Zone	A	B	C	D	E
Date	April 13–21	March 24–30	November 20–28	April 1–8	April 1–8
Temperature in °C	19–21	23–28	18–23	24–26	24–26
Salinity as per cent salt	8.0	4.3	4.1	9.6	9.6
Per cent of surface illumination	100	5	3.5	1.7	0
Total* illumination g cal per cm^2 per hr	95	80	65	110	100
Per cent free O_2 in air	100	<90	<50	<10	<1
Color of zone	Dark brown	Dusky blue-grn	Lustrous blue-grn	Yellowish blue-grn pink below	Pale yellow pink at top
Depth in mm	0–0.5	0.2–2	1–4	3–8	4–12

* Illumination given for 1 hour between 1200 and 1300 hours on an average day during the experiments. These data represent the highest illumination per hour hence greatest light penetration for each period.

Experimental conditions during growth measurements in laboratory

Zone	A	B	C	D	E
Date	April 13–21	March 24–30	November 20–28	April 8–14	April 1–8
Temperature in °C	19–21	23–28	18–23	24–26	24–26
Salinity as per cent salt	2.6 for all gravimetric experiments 1.6 for all morphometric experiments				
Per cent of surface illumination	100	5	3.5	0	0
Total illumination g cal per cm^2 per hr	95	80	65	110	100
Per cent free O_2	21.0	<21.0	<10	0.05	<0.01
Per cent free N_2	78.0	>78.0	>85	99*	99*
Color of zone	Dark brown	Dusky blue-grn	Lustrous blue-grn	Yellowish blue-grn pink at bottom	Pale yellow pink at top

* 1% Argon.

Table 2. Properties of organic matter in sediments from blue-green algal mats (Parker and Leo, 1965).

Location	Organic carbon (%)	C_{16} (0)*	C_{16} (1)	C_{18} (0)	C_{18} (1)
Harbor Island algal mat					
Living mat †	32	3100	560	130	1200
1st mud layer	1.1	1200	330	180	330
2nd mud layer	0.84	200	23	97	n.d.
Baffin Bay core					
0–10 cm	2.0	149	53	53	89
37–41	0.85	192	35	35	50
60–64	1.1	154	6	58	20

* Numbers in parentheses indicate the number of double bonds. † The living mat contained 296 ppm $C_{18}(2)$ and 31 ppm $C_{18}(3)$.

Concentration of the major fatty acids in recent sediments expressed as parts of fatty acid per million parts of organic carbon of each sediment. n.d., not detected.

microcrystalline aragonite intermeshed with mucilaginous organic material and is believed to be directly precipitated from super saturated sea water within the lower mat which may be induced by bacterial action (Dalrymple 1965). The intermittent flooding and drying of the algal flats result in the alternation of sediment and old mat layers beneath the now active mat. Sollins (1969) found 270-640 g/m^2 of organic matter in the top layers and 970-1350 g/m^2 for the entire core. The living mat may contain as much as 32% organic carbon (Parker and Leo, 1965).

Blue-green algal mats may be an important ecosystem in the formation of petroleum. The anaerobic lower mat restricts consumers and favors the deposition of organic matter suitable for oil petrogenesis. A few investigators have studied the types and changes in organic deposition in relation to petroleum formation. All recents sediments and the algal mat itself are rich in fatty acids (Parker and Leo, 1965) (Table 2). With increased depth there is a systematic change in the ratio of saturated to unsaturated acids (Fig. 4). The result is a definite gradient through the mat with the early disappearance of highly unsaturated acids.

Diurnal variations in pH are also large as the result of photosynthesis acting directly on the carbonate fractions. Alkalinity measurements in the water over blue-green mats varied from 2.1 - 2.6 milliequivalents per liter (Odum, Siler et al 1963).

The mat contains a sharp gradient from surface oxidized to lower reduced layers (Fig. 5). The potential between the top and bottom is often as great as 0.5 v. (Armstrong and Odum 1964). This redox gradient is produced by separation of oxygen that rises and reduced organics that remain below (Odum 1967b). There is a diurnal pulse in the voltage (Fig. 6). Sollins (1969) has shown that the daily changes in redox potential directly can be related to the storing and use of oxygen with a model which was the basis of computer simulation (Fig. 7).

The changing oxidation conditions of the mat influence the chemical states of various elements. Sulfur exhibits a gradient of oxidized and reduced forms through the mat with there being high concentrations of H_2S and FeS at depth (Odum, Cuzon Du Rest et al 1963; Dalrymple 1965). The voltage difference from top to bottom may also be important in the transport of nutrients (Armstrong and Odum, 1964; Odum 1967b). Phosphate and Nitrate move upward in the gradient and accumulate on or near the surface and the voltage difference may also be used to organize the mat. Blue-green algae may be moving into position according to charge.

Metabolism

Large amounts of carbon are fixed by the mat system. Measurements of oxygen and pH can be used to calculate metabolism (Figs. 8 and 9). Sorensen and Conover (1962) have recorded values as high as 10% dry wgt./day growth in the photosynthetic zone. In most mats, however, the P/R ratio probably

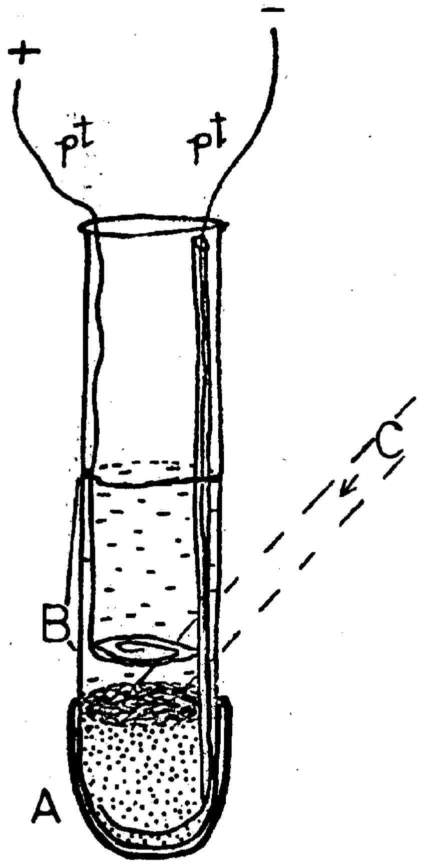
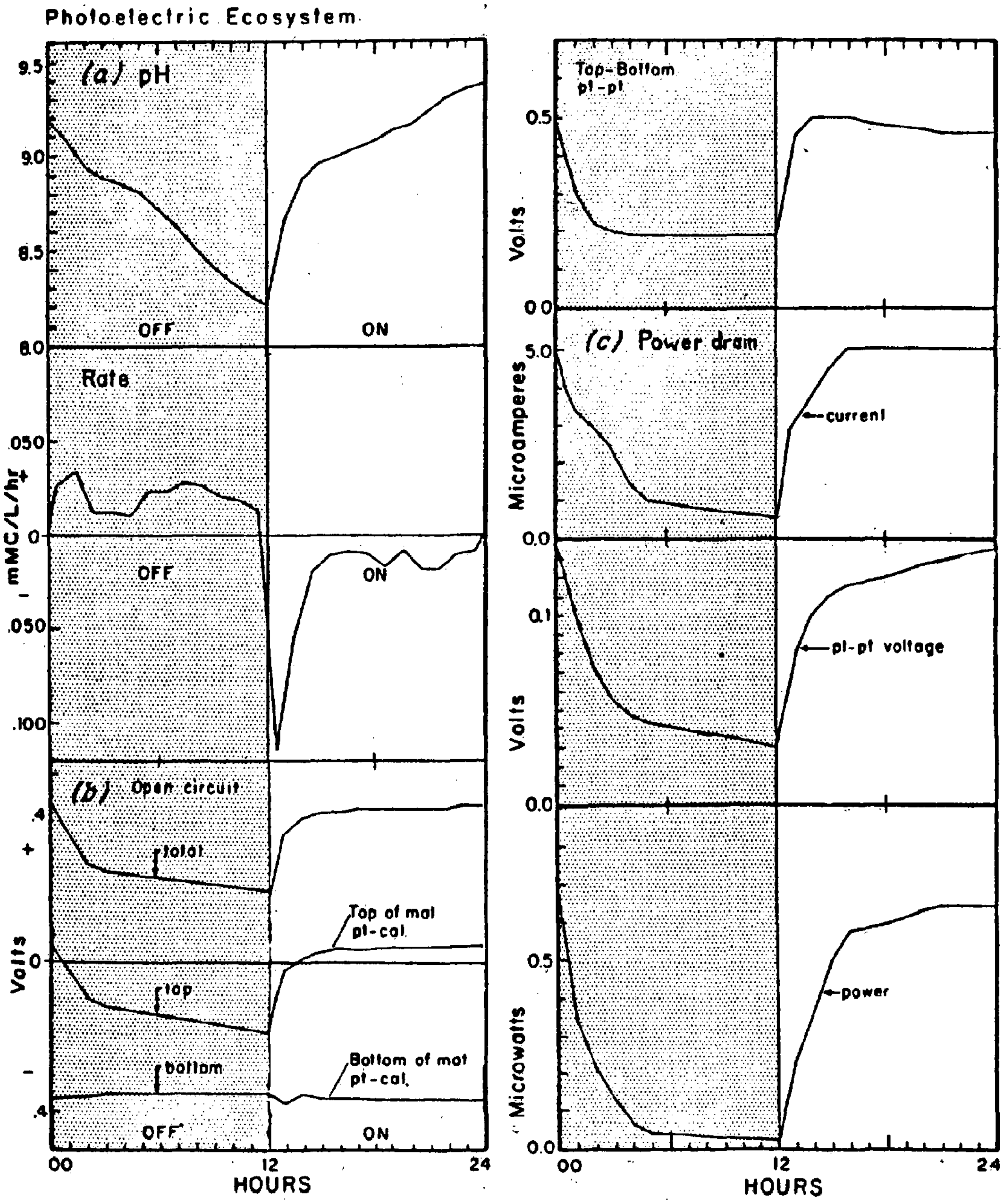


Fig. 5. The blue-green algal mat solar cell. The potential across the electrodes is often as great as 0.5 v. pt (platinum electrodes); A (algal mat and buried (-) electrode); B (water layer and (+) electrode); and C (incident light) (Odum, 1963).



Diurnal record of variables in the blue-green mat ecosystem with a 12-hour day and a 12-hour night. (*a*) The *pH* in the water above the mat and the rate of carbon metabolism computed empirically from the *pH* changes. (*b*) Open circuit voltages (electron voltmeter) with saturated calomel reference electrodes puncturing the mat (bottom left) and across the intact membrane with laterally inserted platinum wire (top right). (*c*) Electrical current, top to bottom potential difference, and external power drain under the loading for maximum power

Fig. 6. Graphs showing the responses of the blue-green algal mat to light (Armstrong and Odum, 1946) (From Armstrong and Odum, 1964; Fig. 1).

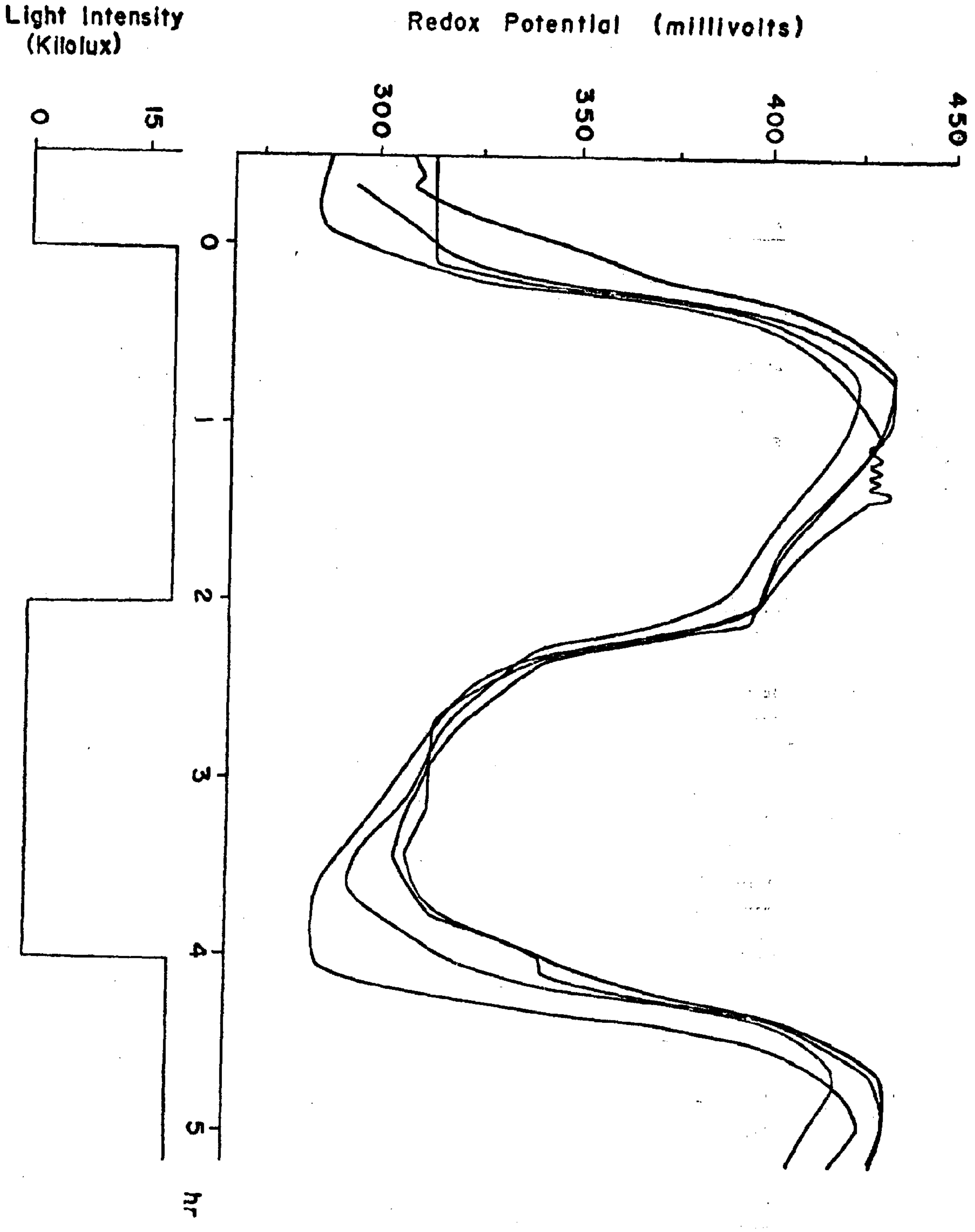
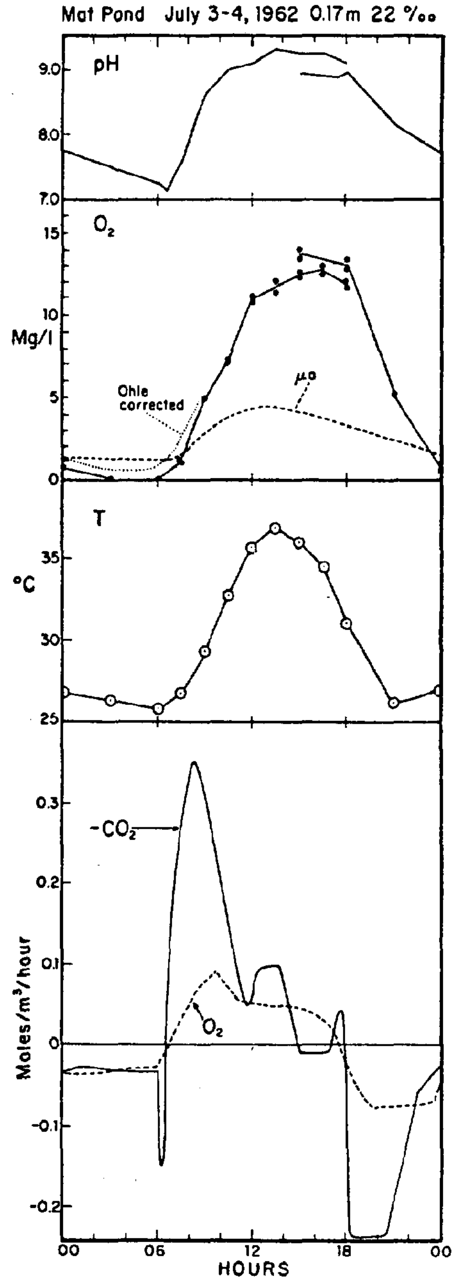
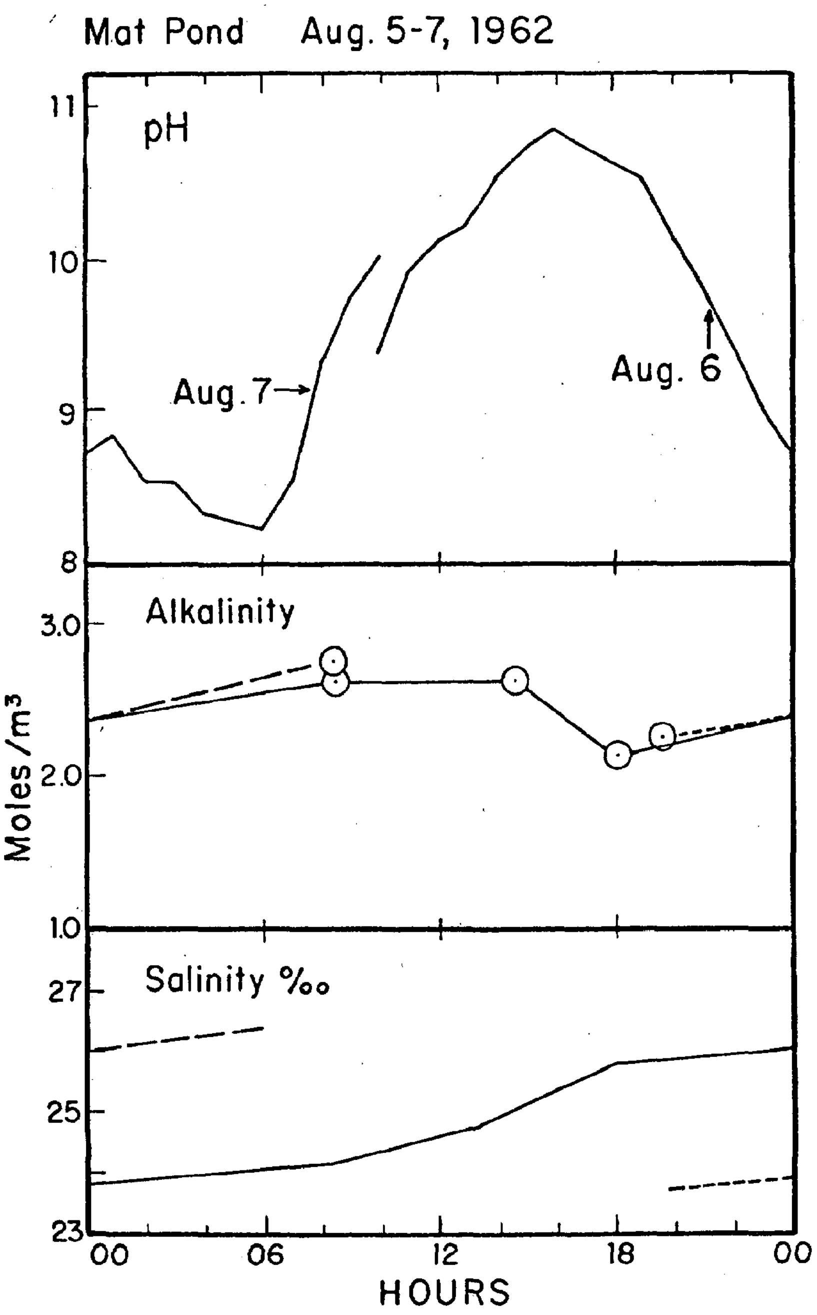


Fig. 7. The relationship of redox potential to light. Each curve represents response in different blue-green algal mat microcosms (Sollins, 1969).



Diurnal record of pH, oxygen concentration, temperature, and carbon and oxygen metabolic rates, July 3–4, 1962, in the blue-green mat pond. Oxygen rate was overcorrected for reaeration by using K_G 1.5.

Fig. 8. Measurement of productivity in the blue-green algal mat (Odum, Siler, et al., 1963).



Diurnal record of pH, alkalinity, and salinity, August 5–7, 1962, in the blue-green mat pond.

Fig. 9. Diurnal change in properties above a blue-green mat (Odum, Siler et al. 1963).

approaches 1.0. Armstrong and Odum (1964) and Beyers (1966) found net production equal to 0.80 mM CO_2/1/2 hr. and nighttime respiration equal to 0.69 mM CO_2/1/12 hr. under 1000 ft-cd. In 600 ft-cd. Sollins (1969) observed net production ranged from 0.52 to 0.76 g. O_2/m^2/d. while total dark respiration accounted for 0.55 - 0.82 g O_2/m^2/d. The P/R ranged from .64 - 1.4 ($\bar{x}$ = .9). Similar measurements have been made by Odum and Wilson (1962), and Armstrong and Odum (1964). The efficiency of production with respect to visible light ranged from 0.5 to 1.62%.

Respiration and photosynthetic quotients may vary greatly over a short period of time. High RQ (1.24 - 3.1) and AQ (4 - 10) possibly reflect processes of delayed oxygen respiration and the asymmetry of the carbon and oxygen processes (Odum, Cuzon du Rest, et al., 1963).

The observed oxygen curve for the first three hours after sunrise remain close to zero suggesting that an anaerobic deficit of reduced compounds were being oxidized by the O_2 as fast as it was being formed. The lower algal cells appear to store reduced substances as O_2 deficits that are made up later. In the determination of productivity values for algal mats corrections should be made for this loss of dissolved oxygen so that diurnal O_2 curves do not underestimate metabolism as measured by carbon (Odum, Siler et al 1963).

Respiration in blue-green mats is a function of the oxygen content during the night and probably also dependent on oxygen tension during the day (Solins 1969). Respiration is greatest about 1/2 hour after dark (5-7 mg. O_2/1 hr.) but drop (1.0 mg/1 hr.) in the early morning. It is probable that respiration is also high during maximum photosynthetic activities.

Under favorable conditions the chlorophyll a content is comparable to some terrestrial forests (Odum, 1967b; Odum et al (1958) record values from 0.28 to 0.75 g./$m.^2$ while Sollins (1969) has measured values up to 2.6 g./$m.^2$ in the top layers.) During unfavorable conditions the chlorophyll a content declines readily and there is remaining a high ratio of carotenoids.

Nitrogen fixation is also well documented among marine blue-green algae but it has not been studied in the algal mat system (Stewart 1962).

Reproduction and Maintenance

When patches of surface mat are lost the newly exposed surface quickly assumes a crustal character. Lyngbya is positively phototrophic in moderate light and possesses some motility (Sorensen and Conover, 1962). The surface mat and open spaces between mats may also be repopulated by hormogones which are bouyant in high saline water.

The extreme diurnal range from aerobic to anaerobic conditions and the varying salinities are undoubtedly the most important factors in controlling biota. Anaerobic night conditions restrict consumers and result in the deposition of organic matter (Odum, Siler, et al.,1963).

The biota associated with the algae may also play an important role in maintainance of the mat. In microcosims the grazing action of dense populations of water bugs caused the mat to lose form and become balls of blue-green algae (Odum 1967b). Where the surface water is deep enough for fish, the carnivore action of Cyprinodon on animal consumers of the blue-green mats acts as part of a self-regulating machinery that permits the mat to hold its organization.

Chapter B-1

MANGROVE SWAMP SYSTEMS

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INTRODUCTION

Long stretches of low-lying tropical and sub-tropical coasts are bordered by dense thickets or forests called mangrove swamps. These swamps dominate the world's coastlines between 25°N and 25°S Lat.; on the east coast of Africa, in Australia, and in New Zealand, however, they extend 10°-15° still further south and in Japan they reach about 7° further north. The brackish waters of estuaries give mangroves their best growth conditions, but they are also well developed in regions of pure sea water, around hypersaline lagoons and salt flats, and up rivers and streams where salt water only occasionally reaches. Thus mangrove swamps on some coasts may be only a narrow fringe whereas elsewhere they spread many miles inland up the tidal rivers. Mangrove swamps are distinct vegetational zones dominated by a few species of moderately large evergreen trees. The term "mangrove" best applies to the whole swamp association, but it is also used in reference to particular species of trees in the swamps. The salient features of mangrove trees were clearly stated by Davis (1940a): "Mangrove plants are typically adapted to fixation in loose, wet soils, a dominantly saline habitat, and periodic submergence by tides. They exhibit different degrees of viviparity of the fruits and seeds and typical xeromorphic adaptations, and have respiratory roots". Mangrove trees so dominate the swamp and have such interesting properties that the autecology of the trees themselves is fairly well known whereas the ecology of associated plants and animals and the energetics of the whole ecosystem are not yet thoroughly understood.

This report concerns mangrove ecological systems, including the distribution, ecology, physiology, geological role, and human use and disturbance. The mangrove swamps of Florida and Puerto Rico are the main subject, but information from other regions will be included.

Appreciation is expressed to Mr. Henry N. McKellar for library assistance and to Dr. H. T. Odum and Dr. William E. Odum for critical reading of the manuscript. Field observations in Ecuador and the Galapagos Islands were made during Stanford Oceanographic Expedition 17 with support from National Science Foundation Grants GB 6870 and GB 6871. Dr. L. G. Hertlein and Mr. D. Chivers kindly identified mollusks and crabs.

DISTRIBUTION

In the United States, the most extensive natural swamps occur in Florida where they cover about 675 square miles (Craighead, 1964). Their best development, in the Ten Thousand Island region and further **southeast** around Cape Sable (Fig. 1), produces a mangrove forest continuous along the coast and extending inland for eighteen or more miles along the water courses (Spackman et al., 1964). Three species of mangrove trees, red mangrove (Rhizophora mangle), black mangrove (Avicennia germinans), (=A. nitida; Moldenke, 1967), and white mangrove (Laguncularia racemosa) dominate the region; buttonwood (Conocarpus erecta), although not a true mangrove, is important in the transition zone between the swamp and upland vegetation (Davis, 1940a). This region is unique because infrequently do red, black, and white mangroves grow so tall. A dense forest of mature red and black mangroves almost 100 feet in height stood here until the violent hurricanes of 1935 and 1960 (Davis, 1940a; Spackman et al., 1964). Further east, mature mangrove swamps are still well developed in the Biscayne Bay--Florida Bay--Florida Keys region but they decline northward toward Jupiter (Fig. 1); they are unimportant beyond Cape Canaveral. On the Gulf of Mexico coast mature swamps decline toward Fort Meyers; Rhizophora becomes much less important further north and Avicennia dominates the swamps. The scattered thickets along the north coast of the Gulf of Mexico and in the Laguna Madre of Texas are composed of Avicennia bushes (Price, 1954 b).

There are still extensive red, black, and white mangrove and buttonwood swamps in Puerto Rico, although the earlier coverage had been reduced to about 16,000 acres by 1940 through unwise exploitation and through habitat destruction by agriculture, dredging, garbage dumps, and real-estate development (Holdridge, 1940). Rhizophora mangle from America and Bruguiera sexangula from the Phillipines, introduced into the Hawaiian Islands in 1902 and 1922, respectively, have become well established and are extending their range (Walsh, 1967).

ZONATION OF MANGROVES

The different species of mangrove trees sometimes grow in randomly mixed associations, but usually different species dominate certain bands or zones which are clearly delimited from the others. This characteristic zonation pattern results from differences in rooting and growth of seedlings and from various competitive advantages which each species has in the several gradients present from below the low water to above the high water lines. Davis (1940a) diagrammed a cross section (Fig. 2a) illustrating the zonal pattern in relation to elevation, tidal coverage, and type of soil in

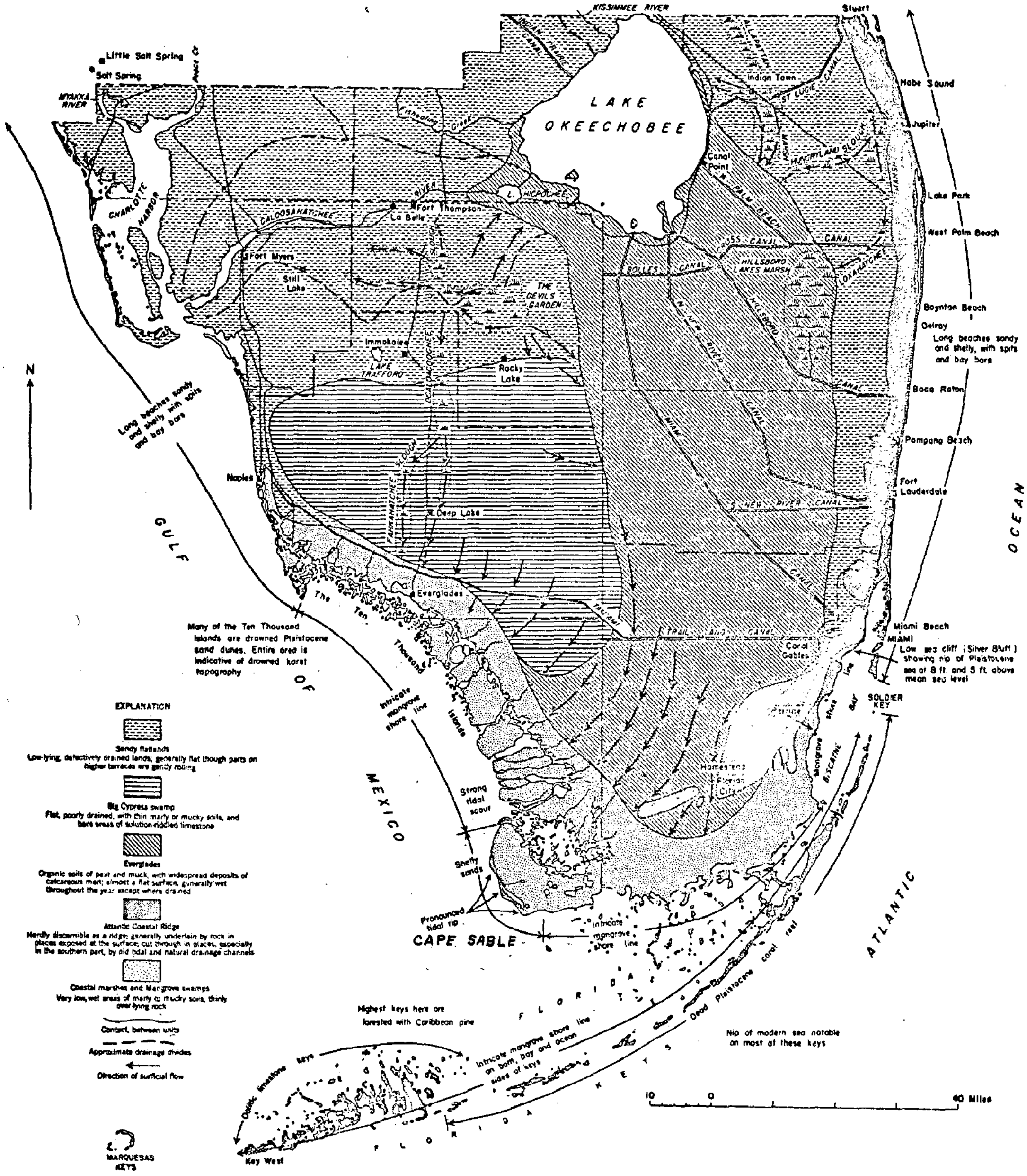
KISSIMMEE RIVER
Stuart
Little Salt Spring
Salt Spring
MYAKKA RIVER
LAKE OKEECHOBEE
Indian Town
ST LUCIE CANAL
Hobe Sound
Jupiter
Canal Point
L. HICPOCHEE
Lake Park
CHARLOTTE HARBOR
RIVER
Fort Thompson
CALOOSAHATCHEE
La Belle
PALM BEACH
CANAL
West Palm Beach
CROSS CANAL
HILLSBORO LAKES MARSH
LOXAHATCHEE
BOLLES CANAL
Fort Myers
Still Lake
THE DEVIL'S GARDEN
Boynton Beach
Delray
Long beaches sandy and shelly, with spits and bay bars
Immokalee
LAKE TRAFFORD
Rocky Lake
NORTH NEW RIVER
HILLSBORO
CANAL
Boca Raton
N
Long beaches sandy and shelly with spits and bay bars
MIAMI CANAL
Pompano Beach
Naples
Fort Lauderdale
OCEAN
SOUTH NEW RIVER CANAL
GULF
Deep Lake
FAKAHATCHEE SLOUGH
The Ten Thousand Islands
Everglades
TAMIAMI TRAIL AND CANAL
Miami Beach
MIAMI
Low sea cliff (Silver Bluff) showing nip of Pleistocene sea at 8 ft. and 5 ft. above mean sea level
Coral Gables
Many of the Ten Thousand Islands are drowned Pleistocene sand dunes. Entire area is indicative of drowned karst topography
OF
Intricate mangrove shore line
SOLDIER KEY
Mangrove shore line
BISCAYNE BAY
EXPLANATION
Sandy flatlands
Low-lying, defectively drained lands; generally flat though parts on higher terraces are gently rolling
Big Cypress swamp
Flat, poorly drained, with thin marly or mucky soils, and bare areas of solution-riddled limestone
Everglades
Organic soils of peat and muck, with widespread deposits of calcareous marl; almost a flat surface, generally wet throughout the year except where drained
Atlantic Coastal Ridge
Hardly discernible as a ridge; generally underlain by rock in places exposed at the surface; cut through in places, especially in the southern part, by old tidal and natural drainage channels
Coastal marshes and Mangrove swamps
Very low, wet areas of marly to mucky soils, thinly over-lying rock
Contact, between units
Approximate drainage divides
Direction of surficial flow
MEXICO
Strong tidal scour
Homestead
Florida City
Shelly sands
Pronounced tidal rip
CAPE SABLE
Intricate mangrove shore line
ATLANTIC
FLORIDA BAY
Dead Pleistocene coral reef
Highest keys here are forested with Caribbean pine
Nip of modern sea notable on most of these keys
Intricate mangrove shore line on both, bay and ocean sides of keys
Oolitic limestone keys
FLORIDA KEYS
10
0
40 Miles
MARQUESAS KEYS
Key West

Fig. 1. Topographic-ecologic map of southern Florida (from Tabb, 1963).

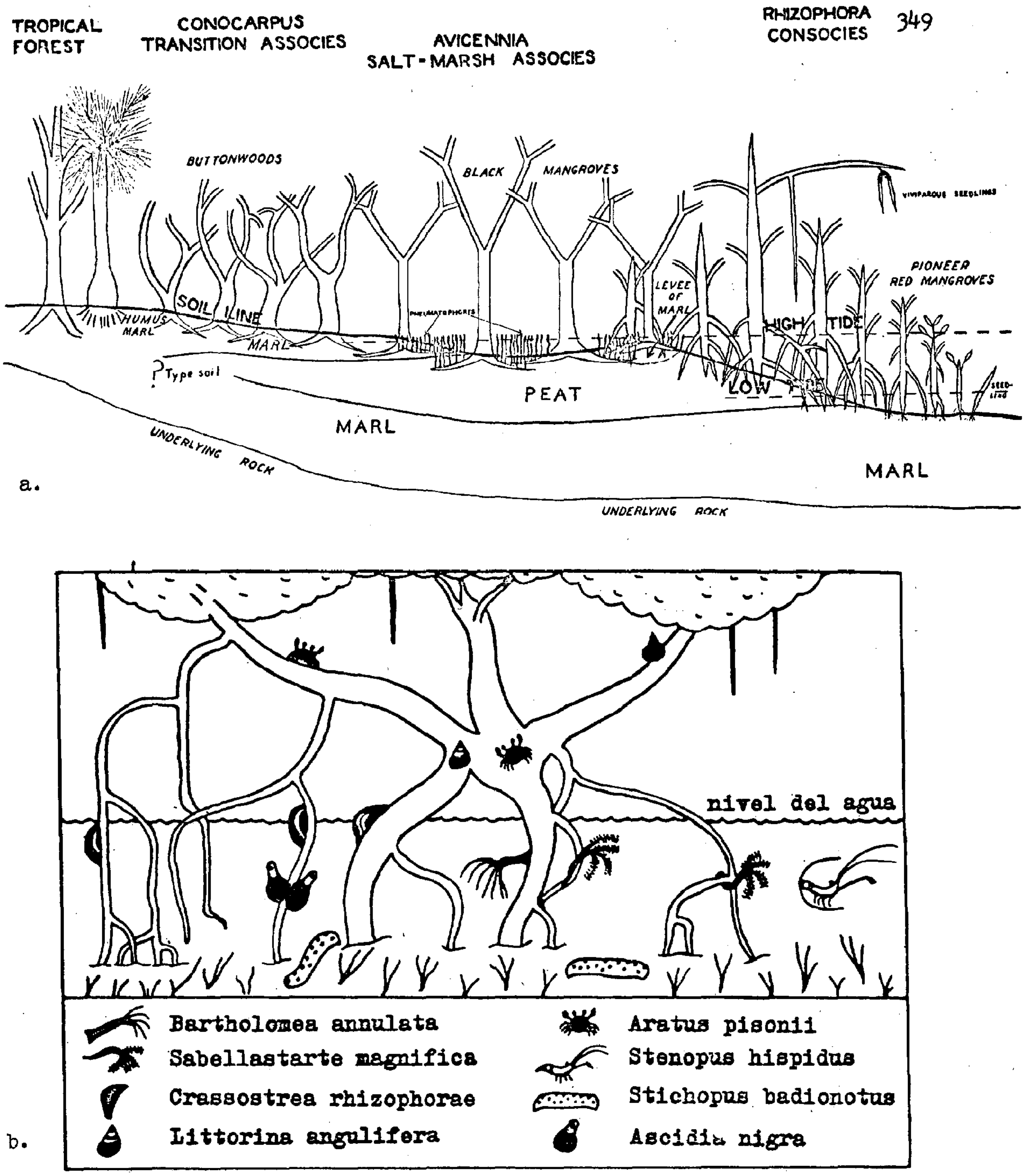
TROPICAL FOREST
CONOCARPUS TRANSITION ASSOCIES
AVICENNIA SALT-MARSH ASSOCIES
RHIZOPHORA CONSOCIES
BUTTONWOODS
BLACK MANGROVES
VIVIPAROUS SEEDLINGS
PIONEER RED MANGROVES
LEVEE OF MARL
SOIL LINE
HUMUS
MARL
PNEUMATOPHORES
HIGH TIDE
LOW TIDE
SEEDLING
Type soil
PEAT
MARL
UNDERLYING ROCK
MARL
UNDERLYING ROCK
a.
nivel del agua
Bartholomea annulata
Sabellastarte magnifica
Crassostrea rhizophorae
Littorina angulifera
Aratus pisonii
Stenopus hispidus
Stichopus badionotus
Ascidia nigra
b.

Fig. 2. (a) Diagrammatic transect of the mangrove communities from the pioneer Rhizophora family to the tropical hammock forest, showing approximate tide levels and soil conditions usually found in a marl soil region (From Davis 1940a).(b) Diagrammatic vertical distribution of fauna in Puerta Rican red mangrove forest (From Glynn 1964).

southwest Florida. Beginning at the right we see Rhizophora mangle seedlings that have sprouted in marl soil below the low tide level; these form the most seaward band. Rhizophora may be easily recognized by its arching prop roots and by the long slender seeds which germinate before dropping from the tree. The prop roots are the most important attachment surfaces for sessile organisms in the intertidal region. To their left, on slightly higher intertidal peat soil is the mature Rhizophora zone; the prop roots of these trees are inundated by almost every high tide. The zone inland is composed of Avicennia trees growing on flat areas flooded by the higher tides (Fig. 2a). Avicennia has characteristic pneumatophores. Large numbers of these slender appendages grow up from the main roots until they emerge from the mud; their respiratory function is discussed below. Still further inland buttonwood swamps and Juncus roemerianus marshes form the transition band between the mangroves and either the tropical forest trees or the sawgrass (Mariscus jamaicensis), plants that are unable to survive significant amounts of salt. Laguncularia is found in all zones but usually not as the dominant; it is often most abundant near the brackish marshes between the Avicennia and Conocarpus zones.

Glynn (1964) diagrammed the vertical zonation of animals at one place in a Puerto Rican swamp (Fig. 2b). Vertical zonation of attached algae is discussed below.

The characteristic zonation and succession seen in Florida swamps is also present in many other estuaries, although the species may be different. For example, in Australia it is Avicennia marina that pioneers and borders the sea while Rhizophora stylosa usually forms the second succeeding band (Macnae, 1967). The subterranean root mat and countless emergent pneumatophores of Avicennia are capable of holding the surface sediments firm, but Rhizophora seedlings sooner or later germinate in the shade of the Avicennia and eventually crowd them out (Macnae, 1967). Further up the estuaries, Rhizophora usually borders the stream bank. In East Africa Walter and Steiner (1936) found sharply defined zones with Sonneratia alba nearest the open water, then Rhizophora mucronata, then Ceriops Candolleana, and finally Avicennia marina nearest the high ground.

ENVIRONMENTAL FACTORS AND SPECIAL ADAPTATIONS

Temperature

Cold weather is the most obvious environmental factor which limits the geographical distribution of mangrove trees and, therefore, the distribution of this type of ecosystem. Mangroves are tropical trees and no species is able to survive hard frosts. The minimum air temperature which they will survive is about 25°F (Davis, 1940a), but Rhizophora seems less resistant than *Avicennia*, perhaps because it does not sprout from the stump (Holderidge, 1940). The northern limit of these species varies from year to year, being pushed southward in cold winters, but moving northward again during warm years following natural dispersal of seeds and resprouting. The effects of environmental factors other than low temperature are difficult to separate and assess individually, but the most important effects will be described here in order to try to evaluate their effects upon zonation and succession in later paragraphs.

Tides

The influence of tides upon mangrove swamps is of prime importance. A large tidal range is not necessary, however; well developed swamps are present in Puerto Rico where the range is less than 1/3 m (Biebl, 1962) as well as in Australia where it exceeds 3 m (Macnae, 1967). Mangroves also line the upper reaches of rivers in the Everglades where the tidal ranges are very small (W. E. Odum, personal communication). In regions of small tidal range, wind may force sea water from one shallow basin to another (Davis, 1940a), or up or down an estuary, against the normal tidal flow. Although generally considered intertidal, mangroves may cover a wider horizontal zone than just between the reaches of low and high water. *Rhizophora* communities, for example, reach into water almost constantly one to two feet deep and *Avicennia* grows at levels flooded only by the highest spring or storm tides (Davis, 1940a). However, in areas where tidal range is large, the seaward margin of the swamp may be above mean sea level (Macnae, 1967) and a zone of bare mud extends down to below the low water line. Tidal action certainly is important in bringing salt water up the estuary against the downward flow of freshwater, and this salt water eliminates competition from fresh water species, both plant and animal. It is the periodic return of the tides that keeps the soil saturated with water, contributing to its anaerobic nature. It also wets the epiphytic algae high on the prop roots. Tidal currents circulate particulate matter for filter feeders such as sponges, oysters, and barnacles; that which is left by the receding water provides food for deposit feeders such as snails and fiddler crabs. Many mangrove swamps produce large excesses of organic matter and some of this is exported on each ebb tide. Finally the tidal movement of water is essential for upstream transport of invertebrate larvae and the seeds of the mangroves themselves. Although some seeds may drop and take root below the parent tree, many of them float away. Seeds of *Rhizophora*, *Avicennia*, and *Laguncularia* may drift for months before taking root far from their source, some upstream, some thousands of miles down the coast or across the sea.

Salinity

Mangrove swamps occur in regions of high, low, or variable salinity. Salinity appears to be of importance not because the salt is necessary for the growth of mangrove trees but because it reduces competition from other species. Rhizophora, Avicennia, and Laguncularia have been grown for two to three years in salt-free water or soil (Bowman, 1917). In natural estuaries, flooding during the rainy season may expose them to nearly fresh water for almost half of the year; alternatively, evaporation during dry weather may create shallow ponds considerably saltier than sea water without causing damage. In Florida the mature Rhizophora swamps along the outer parts of low shores and on shoals in bays generally have a fairly constant salinity; further from the coast they may grow in brackish water, and still further inland unique communities of dwarfed Rhizophora grow in practically fresh water (Davis, 1940a). Egler (1952) suggests that the fires and hurricanes that periodically sweep through this zone destroy the woody stand and sawgrass marsh takes over; because Rhizophora is prolific and aggressive, it invades the marsh first, but may be followed by Avicennia to form a mixed stand again. On the other hand, the early growth of red mangroves is faster in salt water than in fresh waters (Stern and Voigt, 1959). Avicennia frequently grows on flats where evaporation of sea water concentrates the salt, and the soil water salinity may rise above 80°/oo; on the other hand, rain may dilute the surface water to very low values (Davis, 1940a). Laguncularia also is tolerant of wide salinity changes. The algae that grow on prop roots of Rhizophora mangle are able to survive in fresh water, sea water, and 4-fold concentrated sea water (Biebl, 1962). The invertebrates and fishes of the swamps are also relatively tolerant of wide salinity changes. Motile species may avoid sudden reductions in salinity by moving downstream or into deeper, saltier waters. Sessile forms, however, must have physiological or behavioral adaptations that are adequate for most conditions. Unusual rainfalls resulted in mass mortalities of sedentary invertebrates on mangrove roots in Kingston Harbor, Jamaica (Goodbody, 1961).

Giglioli and King (1966) showed the variations in soil water and soil chlorides at different depths in mangrove swamps of west Africa during the dry and wet seasons. In old, stilted Rhizophora soils, water content of the upper foot of soil decreased from about 66% at the beginning of the dry season to about 30% just before the rains (Fig. 3, curve) whereas the water content below one foot was about 40% throughout this period. Soil chlorides varied little during this period (Fig. 3, histograms), apparently because the high permeability allowed equilibration with the waters which flooded the region. In the somewhat higher Avicennia and Sesuvium soils, the high evaporation rate during the dry season caused the soil chloride to become very high (Fig. 3); this salt was eluted again during the rainy season. The deeper layers of Avicennia and Sesuvium soils contained considerably more chloride than the Rhizophora soils. The deep Avicennia soils increased in chloride content during the dry season more than the Sesuvium soils (Fig. 3).

Davis (1940a) made the following conclusions regarding salinity:

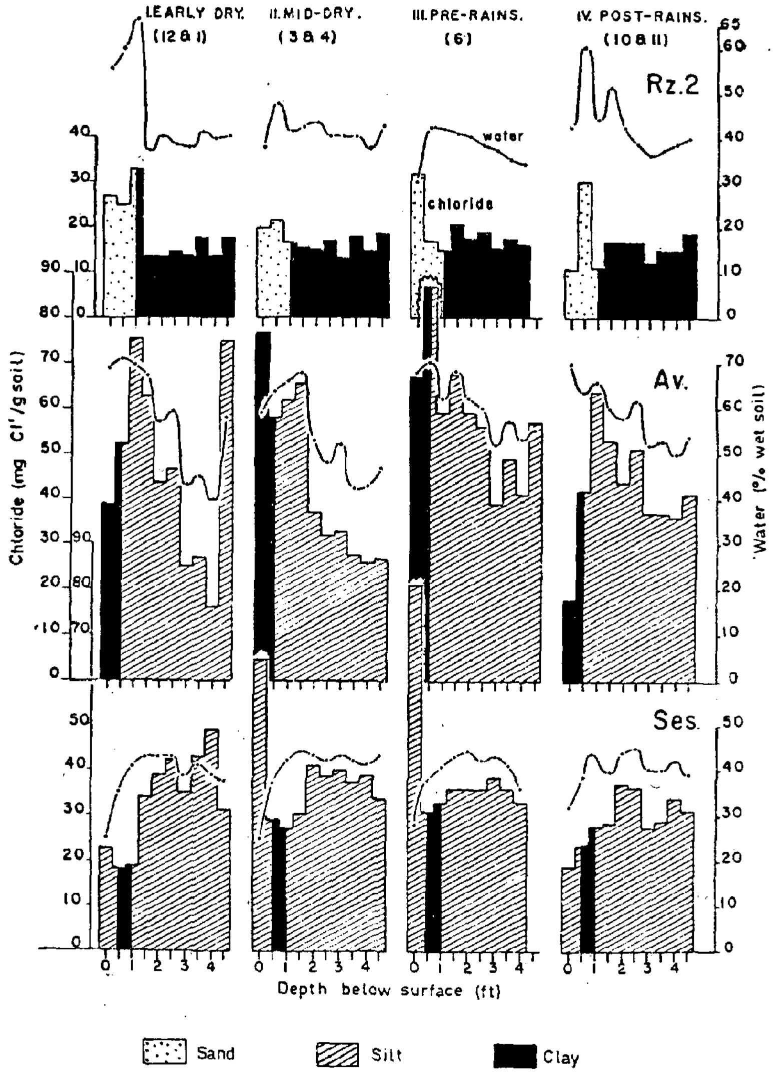

Fig. 3. The seasonal and vertical variations in the concentration of soil chlorides (histogram) and water content (curve) in soils under old Rhizophora, Rz.2; Avicennia, Av. and Sesuvium, Ses. Soil texture down each profile is indicated by shading (from Giglioli and King, 1966).

"1. Salinity fluctuates widely with the seasonal rainfall, and year-round studies are needed to determine the range of conditions in Florida. 2. Only a few salt-marsh and mangrove plants are halophytes that definitely depend upon high salinity. Most of the mangroves are facultative to a wide range of salinity. A brackish condition is most favorable for the optimum growth of mangroves. 3. Although the different species of the mangrove swamps and salt marshes have a wide range of tolerance, the average salinity of the communities is fairly definite, so that zonation corresponds to seasonal averages of the soil-solution and surface-water salinity. 4. The soil solution usually is more saline and fluctuates less than the surface water. 5. The highest salinity is found where the water level is close to the surface of the soil, with consequent high rate of evaporation. Some of the salt marsh plants withstand higher salinities than any of the mangroves. 6. Saline conditions of both surface water and soil water extend farther inland than the normal range of the tide. The low relief of the land prevents rapid leaching out of this salt."

The ability of mangrove trees to grow in sea water is of considerable ecological and physiological interest. Harris and Lawrence (1917) reported that the salt content of mangrove leaves, especially Avicennia, was higher than that of sea water or of typical land plants and suggested that this resulted from rapid transpiration. Two mechanisms for solving the salt problem are found in mangroves, salt exclusion by the roots and salt excretion by the leaves. Salt exclusion appears to be important in species of Rhizophora, Avicennia, and Laguncularia; there is less salt in xylem sap of these three genera than is present in sea water, although there is much more than in ordinary land plants (Scholander et al., 1962). The most recent theory (Scholander et al., 1965) suggests that the negative pressure generated by transpiration in the leaves which draws water up the xylem is sufficient also to separate fresh water from sea water at the roots. This reversed osmosis is therefore proposed as a mechanism for salt exclusion. On the other hand, the leaves of Aegialitis, Aegiceras, and Avicennia secrete excess salt (Scholander et al., 1962). These mangroves are the least able to exclude salt from the roots, but they have effective "salt glands" on the leaves that can excrete solutions containing 2-5% NaCl. This is an active transport mechanism (Atkinson et al., 1967). There is more secretion during the day, probably because of higher transpiration rates, but perhaps also because salt excretion itself is light stimulated (Scholander et al., 1962; Atkinson et al., 1967). The ability of Avicennia to exclude some salt at the roots and to excrete salt by the leaves permits its growth in hypersaline areas. Perhaps the often higher salintiy of mangrove soils and peats than that of the overlying water (Davis, 1940a; Scholl, 1965) may partially result from salt exclusion by the mangrove roots.

The low transpiration rates of mangroves are an adaptation to growth in saline waters. Rhizophora, Avicennia and Laguncularia all have simple fleshy, elliptical or ovate leaves. The structure of the leaves, especially the heavily cutinized epidermis and lack of stomata on the upper surface, tends to restrict water loss (Bowman, 1917). The result is that average daytime values of transpiration for Rhizophora and Avicennia are 6.5 $mg/dm^2 \cdot min.$ and 2.5 $mg/dm^2 \cdot min.$, respectively, values that are low compared to those for other plants (mostly 10-55 $mg/dm^2 \cdot min.$; Scholander et al., 1962). Bowman (1917) found that the rate of transpiration of Rhizophora mangle decreased when exposed to higher salinities. Although the physiological drought of saline soils has necessitated this adaptation in mangroves which is similar to that of desert plants, low transpiration rates are sufficient if essential nutrients are abundant in the soil water. Nutrition of mangroves, however, has not yet been studied under natural conditions.

Temporal Patterns

Cycles of environmental changes are evident both on a short term (daily or tidal) and a long term (seasonal) basis. The daily input of solar heat and the regular return of tidal waters cause a fairly regular pattern of changes in water depth, temperature, salinity, oxygen, and pH. These factors were measured by Orr and Moorhouse (1933) during winter in a pool in a mangrove swamp at the mouth of the Daintree River, Australia. The mangrove area was exposed at low tide, but flooded again at about half tide. The pool bottom was covered by fine mangrove mud, and a thick growth of trees covering the pool allowed only diffuse light to enter. The pool slowly drained during low water, but was refilled again beginning at about 11:00 p.m. and 1:00 p.m. on two successive days (Fig. 4a). Temperature went down at night until the pool was flooded again with warmer water; it went up most rapidly during the noon hours in spite of relatively weak sunlight (Fig. 4, b). Salinity was not affected by evaporation, as was true in another pool they studied, but only by the changes in the river water: sea-water mixture, increasing as the tide rose (Fig. 4, c). The decline in oxygen and pH (Fig. 4, d, e, f), however, resulted predominantly from in situ utilization for animal and bacterial respiration. There was no significant photosynthesis to increase oxygen levels in the daytime, but oxygen was replenished when the pool was flooded each time. Thus the dim light, absence of algae, and abundance of organic matter in the mud make these mangrove areas large consumers of oxygen. In other mangrove pools, photosynthesis of algae may partially offset the respiratory oxygen requirement (Orr and Moorhouse, 1933).

The seasonal cycles of temperature, salinity, pH, and oxygen content of the water in a mangrove-bordered lagoon in Puerto Rico were reported by Mattox (1949). The annual temperature range was only from 25.5° to 30.5°C. Salinity generally ranged from 34 °/oo to 39 °/oo; this small range is attributable to the fact that the lagoon is on the dry end of Puerto Rico and received very little runoff even during the rainy season. pH was nearly constant (7.4-8.2), but oxygen varied by a factor of two throughout the year. The oxygen content was lowest (3.5 mg/l) in late summer when temper-

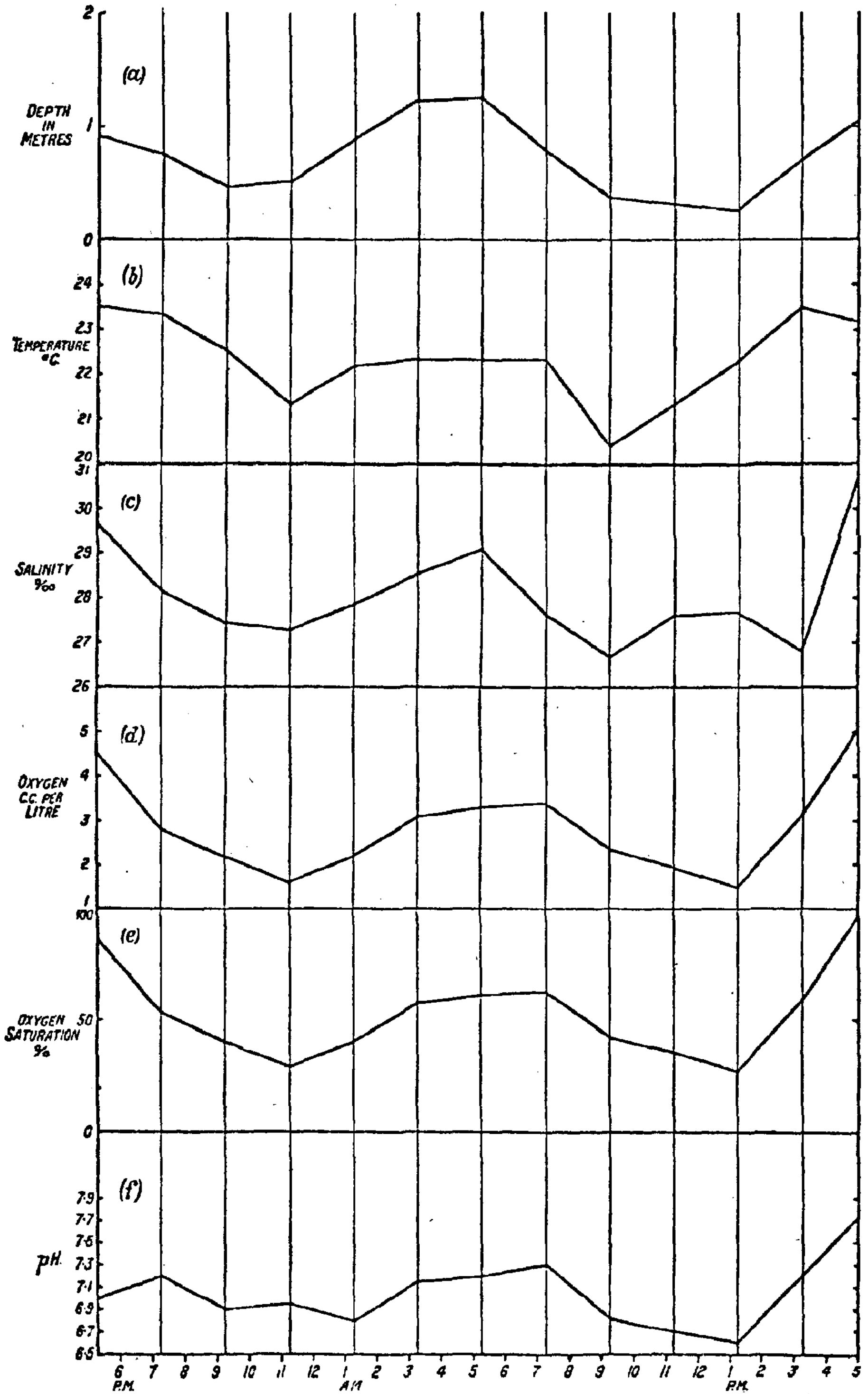

Fig. 4. The diurnal changes in the water of a pool in the mangrove swamp near the mouth of the Daintree River. (a) Depth; (b) temperature; (c) salinity; (d) oxygen content; (e) oxygen saturation; (f) pH value (from Orr and Moorehouse, 1933).

atures were highest, and highest (7 mg/1) in the late winter. Oxygen content of the lagoon was consistently lower than that of the open bay nearby, perhaps because of the continuous input of organic matter from the surrounding mangroves.

Sediments

Mangroves grow on a variety of soils, or even on rock if there are sufficient crevices into which they may fasten their roots. In Florida the primary soils are either calcareous marl muds, calcareous sands in the southern part, or siliceous sands further north. The fine grained marl muds are deposited mostly in protected waters whereas the coarser calcareous sands occur in regions having considerable current action (Davis, 1940a). Mangrove growth is generally better in the marl muds than in other primary soil types. *Rhizophora* and *Avicennia* do well on most soil types except shifting sands where currents are strong; *Laguncularia*, however, thrives on higher sandy soils. Of great importance are the secondary, organic soils of peat or muck that have been deposited in many places. Much of the peat was produced by the mangroves themselves and deep layers may cover any of the primary types or be found interbedded or mixed with marls or sands (Davis, 1940a). Peat soils several meters thick represent the accumulated plant growth of long periods of time during which decomposition was slow. The finding of *Avicennia* peat deposited over *Rhizophora* peat demonstrates the same successional pattern, namely that *Rhizophora* is the pioneer, seen in the zonal pattern (Fig. 2a).

Thornton and Giglioli (1965) made a detailed study of the changes in pH as various types of mangrove soils were dried; the pH usually dropped very low, but the amount of change depended on the soil type. Because of this, the fibrous peat soils developed by *Rhizophora* forests are not easily converted into agricultural land; drainage allows oxidation of sulfides and the resulting acidity prevents successful rice growth such as is possible on soils previously covered by *Avicennia* (Hesse, 1961b).

Water Table and Soil Aeration

The distribution of mangrove species is related to the water level in the soil (Fig. 2a). The pioneer *Rhizophora* plants grow in water that averages 16 inches deep, mature *Rhizophora* in water 10 inches deep, and *Avicennia* in water only 6 inches deep (Davis, 1940a). The actual water depth over the soil varies, of course, with the stage of the tide or the amount of recent rainfall, runoff, or evaporation, but the soils on which *Rhizophora* and *Avicennia* grow are usually saturated. The transition species *Conocarpus*, however, grows on soil where the water table is usually only about 4 inches below the surface and capillarity keeps the upper few inches moist.

Aeration is very slow in fine sediments that are saturated, and consequently mangrove soils are usually low or lacking in oxygen necessary for respiration of the living tissues of the roots. Oxygen from the air is not primarily supplied through the soil, but through open, spongy passages in the roots. Above the mud, the prop roots of red mangroves have many small pores, called lenticels, and when low tide exposes these lenticels, oxygen passes in and diffuses rapidly to all parts of the living, buried root (Scholander, et al., 1955). Black mangroves do not have these prop roots, but their roots extend underground in all directions from the main trunk. To obtain oxygen, their roots send special structures, called air-roots or pneumatophores, straight up 20-30 cm above the mud surface. During low tide, when the lenticels are exposed to air, oxygen enters and spreads down to all the metabolizing tissues of the roots (Scholander, et al., 1955).

SUCCESSION

Each species of mangrove tends to change the characteristics of the area where it grows; the new conditions may be better for another species which will then come in and supplant the first. This pattern of one species replacing another in time, called succession, is clearly seen in the distribution pattern in Florida (Fig. 2a). Colonization of almost constantly submerged shoal areas and the lower banks of tidal creeks usually begins when seeds of Rhizophora take root. As these pioneer trees grow, adventitious roots sprout from the stems to form arching prop roots; later drop roots also grow down from the horizontal branches until each tree has many stems. Some of these drop roots take root in water too deep for seedlings to prosper. The stems and prop roots form a dense tangle and are encrusted with algae and with sedentary animals such as oysters and barnacles. Marine benthic algae and two species of higher plants, Thalassia testudinum and Cymadocea manatorum, grow in shoal areas near the red mangroves (Davis, 1940a). Debris is trapped and sediments accumulate among the stems because of reduced water currents, and the depth of the water gradually decreases. Furthermore, organic soil (peat) formed by leaves, roots, and stems of Rhizophora itself also contributes to building up of the soil surface. Geological uplift or a general lowering of sea level may also be involved in raising the Rhizophora zone above its optimal elevation.

As the water becomes shallower, growth conditions become more favorable for Avicennia. The Avicennia zone, then, tends to succeed the Rhizophora zone in time and in space (Fig. 2a, 5). The invading Avicennia and a variety of salt marsh plants (Batis maritima, Salicornia perennis, Monanthochloë littoralis, Sporobolus virginicus, Spartina alterniflora, and S. spartinae) form a relatively open, shallow, swamp-marsh association which continues to accumulate debris, sediments, and organic detritus and consequently gradually becomes still shallower and more stagnant. Dry periods cause salinities to go up, whereas rainy weather may wash most of the salt out of the region; salinity is therefore highly variable (Fig. 3). The Avicennia trees in some places grow to more than a foot in diameter, but in other

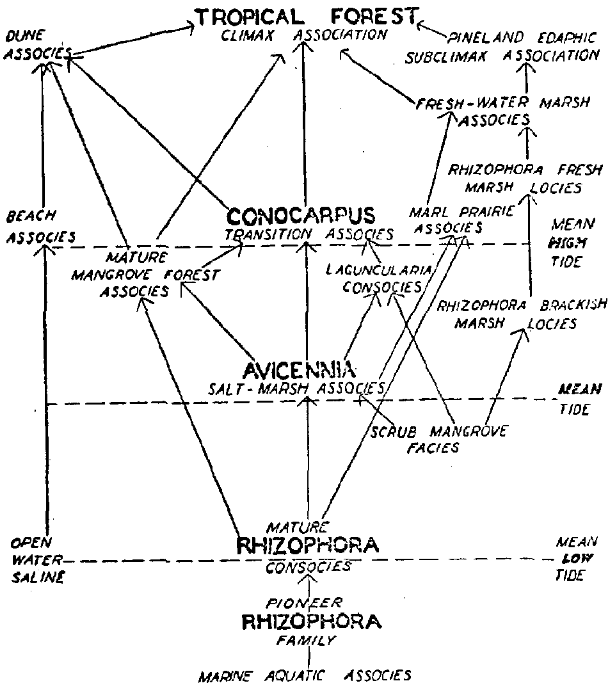
TROPICAL FOREST
CLIMAX ASSOCIATION
DUNE ASSOCIES
PINELAND EDAPHIC SUBCLIMAX ASSOCIATION
FRESH-WATER MARSH ASSOCIES
RHIZOPHORA FRESH MARSH LOCIES
BEACH ASSOCIES
CONOCARPUS
TRANSITION ASSOCIES
MARL PRAIRIE ASSOCIES
MEAN HIGH TIDE
MATURE MANGROVE FOREST ASSOCIES
LAGUNCULARIA CONSOCIES
RHIZOPHORA BRACKISH MARSH LOCIES
AVICENNIA
SALT-MARSH ASSOCIES
MEAN TIDE
SCRUB MANGROVE FACIES
OPEN WATER-SALINE
MATURE
RHIZOPHORA
CONSOCIES
MEAN LOW TIDE
PIONEER
RHIZOPHORA
FAMILY
MARINE AQUATIC ASSOCIES

Fig. 5. Successional relations of mangrove communities and some of the associated plant communities. Approximate tide levels are indicated (from Davis, 1940a).

places they are only small gnarled bushes (Davis, 1940a). Continued elevation of the soil surface creates conditions wherein *Avicennia* does not replace itself and succession may proceed toward a freshwater sawgrass marsh association, a *Laguncularia* community, or a *Conocarpus* association which can still later be replaced by upland tropical forest or pineland (Fig. 2a, 5). Soil borings confirm the pattern of succession. Mangrove peat is found under upland hardwood forest soils, *Avicennia* peat is found under *Conocarpus* soils, and *Rhizophora* peat is found under *Avicennia* soils (Davis, 1938).

If sea level rises or the land subsides slowly, accumulation of peat may keep raising the mangrove associations to a satisfactory height relative to water level. Thick layers of peat are eventually laid down. However, a rapid rise in sea level may force a retreat of all zones inland and peat deposits become buried under maritime sediments. Mangrove peat buried under calcareous mud on the bottom of Florida Bay and also about 1.5 miles off the well-developed modern swamps near Cape Sable is convincing evidence that mangroves are capable of moving landward as well as seaward, depending upon sea level changes relative to the shore (Spackman, et al., 1964). Egler (1952) feels that the botanists have overemphasized the geological importance of mangroves. Without doubt, mangroves oppose the erosive forces of wind and wave and they may build up considerable layers of peat and sediments, but compared to large-scale physiographic processes they are relatively impotent.

ASSOCIATED BIOTA

The mangrove trees themselves are certainly the dominant producers in the swamps, but algae also are important, especially because their production may be much more quickly consumed by the mangrove fauna than the woody materials produced by the trees. In Florida, open shoal areas below mean low water are often covered by tropical species such as *Caulerpa*, *Acetabularia*, *Penicillus*, *Gracilaria*, *Halimeda*, *Sargassum*, and *Batophora* (Davis, 1940a; Taylor, 1954, 1960a). Above this region, on the intertidal muds one may find a thick growth of *Vaucheria* or *Cladophoropsis* (Taylor, 1954). There is also a subterranean algal flora composed of unicellular and filamentous blue-green and green algae (Marath, 1965). The prop roots of *Rhizophora mangle* have several zones of algae attached to them. In Puerto Rico, the permanently submerged portions of the roots often have rich growths of *Acanthophora*, *Spyridia*, *Hypnea*, *Laurencia*, *Wrangelia*, *Valonia* and *Caulerpa*; the intertidal zone may be covered by species of *Murrayella*, *Centroceras*, *Polysiphonia*, *Enteromorpha*, and *Rhizoclonium*; finally, there may be species of *Catenella*, *Caloglossa*, and *Bostrychia* at the upper limit of high tide (Almodovar and Biebl, 1962). Biebl (1962) showed that epiphytic algae of the intertidal zone received only 8% or less of open sunlight because of the *Rhizophora* shade; nevertheless they survived full sunlight longer than the epiphytic algae that grow permanently submerged. Furthermore, the intertidal epiphytics generally were more resistant to osmotic shock, drying, and unusually low or high temperatures than were the submerged algae; this hardiness undoubtedly is of survival value during low tide periods. Species of *Bostrychia*, *Catenella*, *Caloglossa*, and *Murrayella* form a characteristic association (*Bostrychietum*) on mangrove roots around the world (Post, 1936).

Many kinds of animals are found in mangrove swamps, in sharp contrast to the low diversity of plant species. The most important benthic marine animals are probably crustaceans and mollusks and most of these can be classified as either deposit or filter feeders. Fiddler crabs (*Uca* spp.) in Puerto Rico frequently are dominant in terms of biomass (Golley, *et al*., 1962). The crabs on intertidal flats of mangrove islands in Florida bay include *Uca pugilator*, *U. speciosa*, *U. thayeri* and *Eurytium limosum*; other species, *Aratus pisonii*, *Sesarma curacaoense*, and *S. reticulatum* are abundant in mangroves above high water (Tabb, *et al*., 1962). At low water fiddler crabs move out of their burrows to feed on surface deposits; the burrows probably effect some aeration and mixing of the soil (Davis, 1940a). Barnacles such as *Balanus eburneus* attach to roots and stems where they can filter their food from the water at high tide. Coon oysters (*Ostrea frons*), also important filter feeders, are abundant on mangrove roots in Florida and the weight of their shells may eventually cause the root to break off (Davis, 1940a). Another oyster, *Crassostrea virginica*, is important in the intertidal area and below the low water mark in Florida Bay (Tabb, *et al*., 1962). The dead shells and undigested food of these barnacles and oysters contribute to the sediments of the swamp. Several kinds of snails (*Cerithium*, *Melogena*, *Cypraea*, and *Littorina angulifera*) feed on material deposited on the roots or on the mud surface (Davis, 1940a; Tabb, *et al*., 1962). Some vertebrates of the Florida swamps include turtles, crocodiles, alligators, bears, wildcats, puma, and rats (Davis, 1940a). Birds are discussed below. Other important consumers in Florida swamps are amphipods, isopods, the crab *Rhithropanopeus harrissii*, and fishes, especially *Cyprinodon variegatus*, *Mollinesia latipinna*, and *Floridichthys carpio*; Odum (1970) gives food habits of more than eighty species of animals from the swamps.

Mattox (1949) made an intensive study of the oyster, *Crassostrea rhizophorae*, which grows on red mangrove prop roots in Puerto Rico. Physical conditions in the lagoon water were mentioned above. Associated with the oysters on these roots are many other marine invertebrates--sponges, flatworms, hydroids, bryozoans, annelid worms, barnacles, shrimps, crabs, snails, clams, mussels, sea urchins, and tunicates. Thus, this association is a very crowded one, with each individual competing for space and, undoubtedly, also for food. In spite of the crowding, however, the oysters reach market size in 6 to 7 months after setting. Glenn (1964) gave a popular account of the distribution and natural history of invertebrates in Puerto Rican swamps; a sketch of vertical zonation of animals is shown in Fig. 2b. Warner (1967) described the life history of the mangrove tree crab, *Aratus pisonii* and Feliciano (1962) reported on the biology of *Cardi-*

soma guanhumi.

The zonation of animals which parallels the plant zones was described by Macnae and Kalk (1962) in swamps of Mozambique, Africa. There the crabs *Sesarma meinerti*, *S. eulimene*, and *Uca annulipes* were present in the landward *Avicennia marina* fringe. In the zone characterized by *Ceriops* and *Bruguiera* plants, the crabs were *Uca chlorophthalmus*, *Sesarma guttata*, *S. catenata*, *Ilyograpsus rhizophorae*, *Paracleistosoma fossula*, *Eurycarcinus natalensis*, *Metopograpsus messor*, and *Macrophthalmus depressus*. In the *Rhizophora mucronata* zone *Uca urvillei*, *U. chlorophthalmus*, and *Ilyograpsus rhizophorae* were found, whereas the crabs in the channels below the *Rhizophora* zone consisted of *Scylla serrata* and *Thalamita crenata*. Other important animals include the snails *Littorina scabra* and *Cerithidea decollata* on the lower branches of the trees, and *Terebralia palustris* and *Cassidula labrella* on the sediment surface. The very interesting mud-skipper fish, *Periophthalmus sobrinus* was found on the muddy banks of channels in the *Rhizophora* zones, along with the sea cucumbers *Holothuria parva* and *Chiridota* sp. Many species of fishes, shrimp, and insect larvae are found in the channels and can move into the swamps during high water. Finally, barnacles and oysters (*Balanus amphitrite* and *Crassostrea echinata*, respectively) are abundant on the lower trunks and pneumatophores of the trees. Most of these animals do not obtain food directly from the mangroves but either filter their food from the water at each high tide or else they scrape off sediments and surface debris to obtain organic matter. The mangrove trees in the swamp, therefore, serve the animal populations more as a place to live than as a direct source of food. Hence Macnae and Kalk (1962) postulated that the animals were "only fortuitously associated with mangrove trees and that their distribution is controlled by: (i) level of water table, (ii) resistance to water loss, and (iii) correlated with this, the demand for protection from the sun, (iv) the degree of consolidation of the substratum, and (v) the availability in the upper layers of the substratum of a microflora and microfauna and of organic debris suitable for food." These factors, however, seem to be very powerful and there is a remarkable resemblance between the faunas of similar areas in Mozambique and in Java (Verwey, 1930; Macnae and Kalk, 1962).

Two other factors, the strength of current flow and turbidity of water, are probably important in determining whether filter feeders are more important than deposit feeders in mangrove swamps. In the Galapagos Islands I observed that strong flows of water permitted development of filter feeding oysters, mussels, and barnacles (*Ostrea palmula*, *Isognomon chemnitzianus*, *Brachydontes sp.*, *Balanus trigonus* (?), and *Tetraclita squamosa* whereas in quiet backwaters the most important animals were predaceous or deposit feeding crabs and snails (*Uca galapagensis*, *Leptodius snodgrassi*, *Ozius tenuidactylus*, *Mithrax nodosus*, *Chiton sulcatus*, *Thais sp.*, and *Mitra tristis*.) A great deal of work remains to be done in the Florida mangrove swamps, not only to determine distribution patterns, but also to measure environmental requirements, biomass of the important species, food chains, energy flow, and nutrient cycles.

Birds are abundant, conspicuous, and probably important in mangrove swamps; in Africa, Cawkell (1964) reported 45 species whereas in Surinam (Haverschmidt, 1965), and Trinidad (French, 1966) about twice as many were found. Approximately half of the species utilize the swamps for nesting activities and the others feed there or congregate there in large communal roosts. The food resources of the birds are varied. Many (egrets, herons, ibis, ducks, kingfishers, crab hawks, stilts, and pelicans), feed on estuarine fishes and invertebrates, others (fly-catcher, woodpeckers, wrens, swallows, and warblers) feed on insects in the forest, and a few (doves and blackbirds) feed on seeds outside the swamps but return for roosting or nesting. The mangroves themselves and their fruits, however, do not supply nutriment directly and the food supply for birds, like that of the other animals, comes predominantly from marine life in the channels or on the mud flats. The dense nesting colonies in some areas may harm the trees physically, but the excreta probably is of some benefit.

The plankton of mangrove areas has been studied to only a limited degree. It probably contributes only a small amount to the total primary productivity but it does constitute, with detritus, the diet of filter feeders and, after sedimentation, deposit feeders of the swamps. Mattox (1949) found a relatively low (compared to temperate waters) but constant amount of plankton in a Puerto Rican lagoon. The samples were dominated by diatoms, especially species of Thalassiothrix, Chaetoceras, Nitzschia, Skeletonema, and undetermined filamentous types. Animals such as ciliates, foraminiferans, copepods, and invertebrate larvae were present in smaller numbers than the plants. Very large quantities of organic detritus were also present in the water and this detritus was found along with phytoplankton in the stomachs of oysters growing on mangrove roots. Davis and Williams (1950) found a wide variety of both phytoplankton and zooplankton in Florida swamps. He postulated that fresh-water forms are eliminated whenever salinities increase sufficiently and that salt-water forms similarly decline during low-salinity periods. Reinvasion and growth restocks each population when conditions permit. Thus inability to endure salinity stress distinguishes much of the plankton from the mangrove trees, attached algae, and estuarine invertebrates. Studies of standing crops and of productivity would contribute substantially to our knowledge of energetics of the whole mangrove swamp ecosystem.

PRODUCTIVITY

Mangrove forests are among the most productive of all estuarine ecosystems. Golley et al., (1962) made a study of the structure and metabolic rate of a red mangrove forest in Puerto Rico. The mean weights of various parts of the trees from the top down, expressed as grams dry weight/m^2, were: 778 g of leaves, 1274 g of branches, 2796 g of tree trunks, 1437 g of prop roots, and about 5000 g of roots. The animals of this *Rhizophora* swamp weighed only 6.4 g/m^2. About 80% of the leaves were between 4 and 8 m above the forest floor; they were exposed to the brightest sunlight and intercepted about 80% of the light (Fig. 6a). Shade leaves and seedlings were less abundant and were exposed to lower light intensities. About 89% of the photosynthesis was carried on by the sun leaves, and the gross production in May amounted to 8.23 g of carbon/m^2 per day (Fig. 6b, right half). Gross production of this magnitude is characteristic of a fertile ecosystem. In other words, this red mangrove forest fixes as much energy as many other estuaries, eutrophic ponds, evergreen forests, or good farmland (Odum, 1959). Mangrove sun leaves accounted for most of the respiration also; oxygen consumption through the lenticels of the prop roots was also high, reflecting the respiration of the underground roots (Fig. 5b, left half). The export of particulate organic matter was relatively large. Not shown in Fig. 6 are amounts of organic matter in leaves that fall to the soil surface (0.65g C/m^2 · day), the organic matter converted to wood for tree trunks (0.4g C/m^2 · day), and production by algae in the mud surface (0.38 g C/m^2 · day). Animal respiration 0.082g C/m^2 · day) was a very small part of the total. It appears from the close balance between photosynthesis and respiration that this forest was not making rapid net growth during the study period. Other workers (Holderidge, 1940; Noakes, 1955) reported wood production of *Rhizophora* spp. can be at least 10-fold more rapid than that measured by Golley *et al*., (1962). These higher rates of wood production would place *Rhizophora* among the moderately fast-growing tropical hardwood species.

Leaves and twigs constitute a substantial portion of the annual production of mangroves and they form a major source of detritus for the aquatic food chains of a swamp in southwest Florida (Heald, 1969). Only about five percent of the annual leaf production was consumed by terrestrial animals. Some leaves fell throughout the year, but many more dropped in summer than in other seasons. Red mangroves, the dominant in this swamp, dropped about 880 g (dry weight) of leaves, twigs, and other debris annually per square meter of forest; this amounted to 570 g/m^2·yr for the total area of the swamp, including open water areas (Heald, 1969). Red mangroves were the biggest contributors to the debris in the swamp; phytoplankton, *Juncus* and *Mariscus* marshes, and attached algae were only small contributors to the total productivity. The debris decomposed into detritus, the most rapid rate of degradation being found in brackish water and slower rates in fresh water or subaerial conditions. Although the amount of debris remaining became less and less, the amount of protein increased from 3% to 22% in one year, presumably because of the buildup of bacterial and fungal populations (Heald, 1969). Detritus levels in swamp waters were high (49-93 mg/l) from November through February, the beginning of the dry season, and

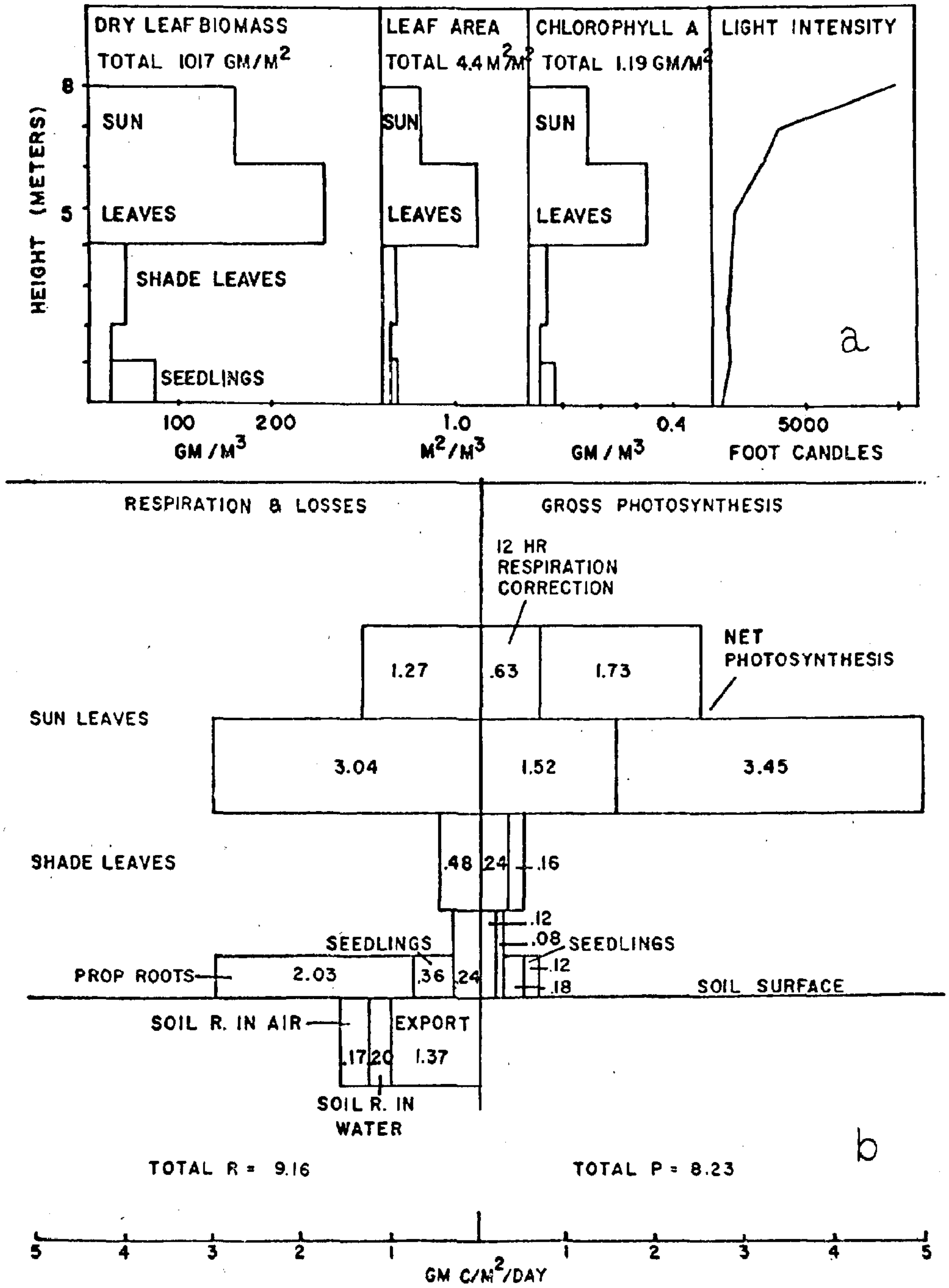

Fig. 6. Red mangrove forest in May. (a) Vertical distribution of leaf biomass, leaf area, chlorophyll *a*, and light intensity. (b) Rates of photosynthesis, respiration, and export (g C/M^2·day) (from Golley, *et al.*, 1962).

were low (2-23 mg/l) during the rest of the year. From 35 to 60 percent of the total suspended matter in the swamp waters came from red mangrove debris; sawgrass, Juncus fecal material, and organic aggregate constituted the remainder (Fig. 7). About half of the annual production of debris was transported to nearby marine bays.

The final steps in the detritus food web were delineated in the same swamp system by W. E. Odum (1970). He examined the stomach contents of more than eighty species of animals and on this basis classified them into appropriate trophic levels. The primary food source for the aquatic animal community was vascular plant detritus, mostly from red mangrove leaves. The major flow of energy to mangrove swamp animals is from mangrove leaves, via degradation and protein enrichment by fungi, bacteria, and protozoa, to a large group of omnivores (Fig. 8; Odum, 1970). These animals ingest some algal material along with the mangrove detritus, they re-utilize some fecal matter, and they prey upon each other. They, in turn, are preyed upon by gamefishes such as tarpon, snook, ladyfish, grey snapper, sheepshead, spotted seatrout, red drum, crevalle jack, gafftopsail catfish, and jewfish. The production of gamefishes is thus directly linked, by way of detritus feeders, to the productivity of red mangrove trees and destruction of mangrove forests will ultimately result in the decline of these fishes (Odum, 1970). Unfortunately, few other studies of mangrove swamp productivity have been made and it is not yet possible to report the productivity of other species, nor the effects of season, sediment type, salinity, or other environmental factors on the rate of organic matter production by mature forests. Of considerable ecological interest is the fact that virtually all of this primary productivity is carried on by a single species, just as in temperate salt marshes Spartina completely dominates and is highly productive. Furthermore, remarkably few animals in the swamp subsist directly on living mangrove tissues; most of the organic matter fixed by mangroves is either deposited as peat, partially decomposed and consumed in the form of detritus, or exported from the swamp by river and tidal currents.

The processes of organic decomposition, detritus production, and nutrient regeneration are important. The slow diffusion of oxygen into sediments results in slow breakdown of organic debris and eventually peat deposits are formed in spite of tropical temperatures. Kohlmeyer (1968) reported that true marine fungi grow on the submerged portions of Rhizophora prop roots and that indigenous floras exist; Trematosphaeria mangrovis is found in Africa on Rhizophora racemosa whereas Didymosphaeria rhizophorae is found in America on R. mangle.

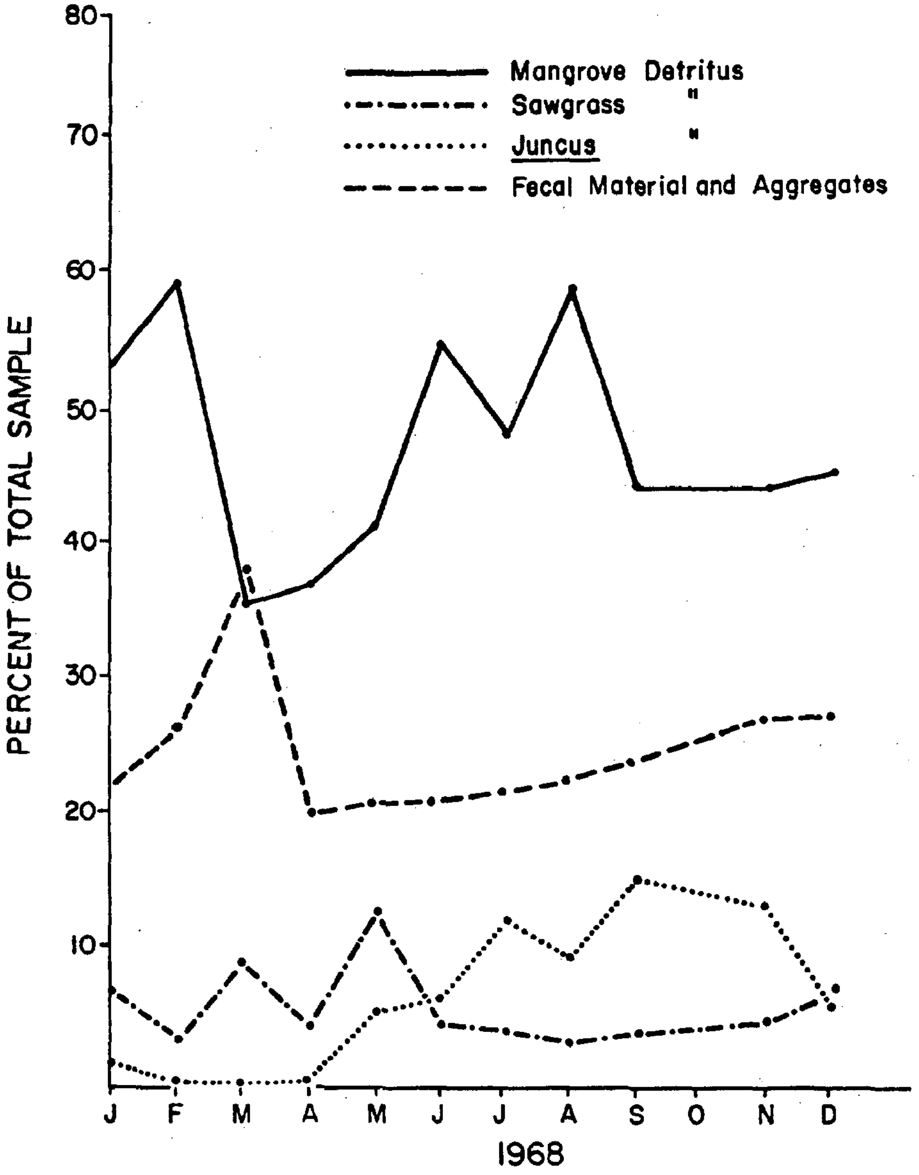

Fig. 7. Percentage contribution of four major sources of detritus in estuarine water samples (Heald, 1969).

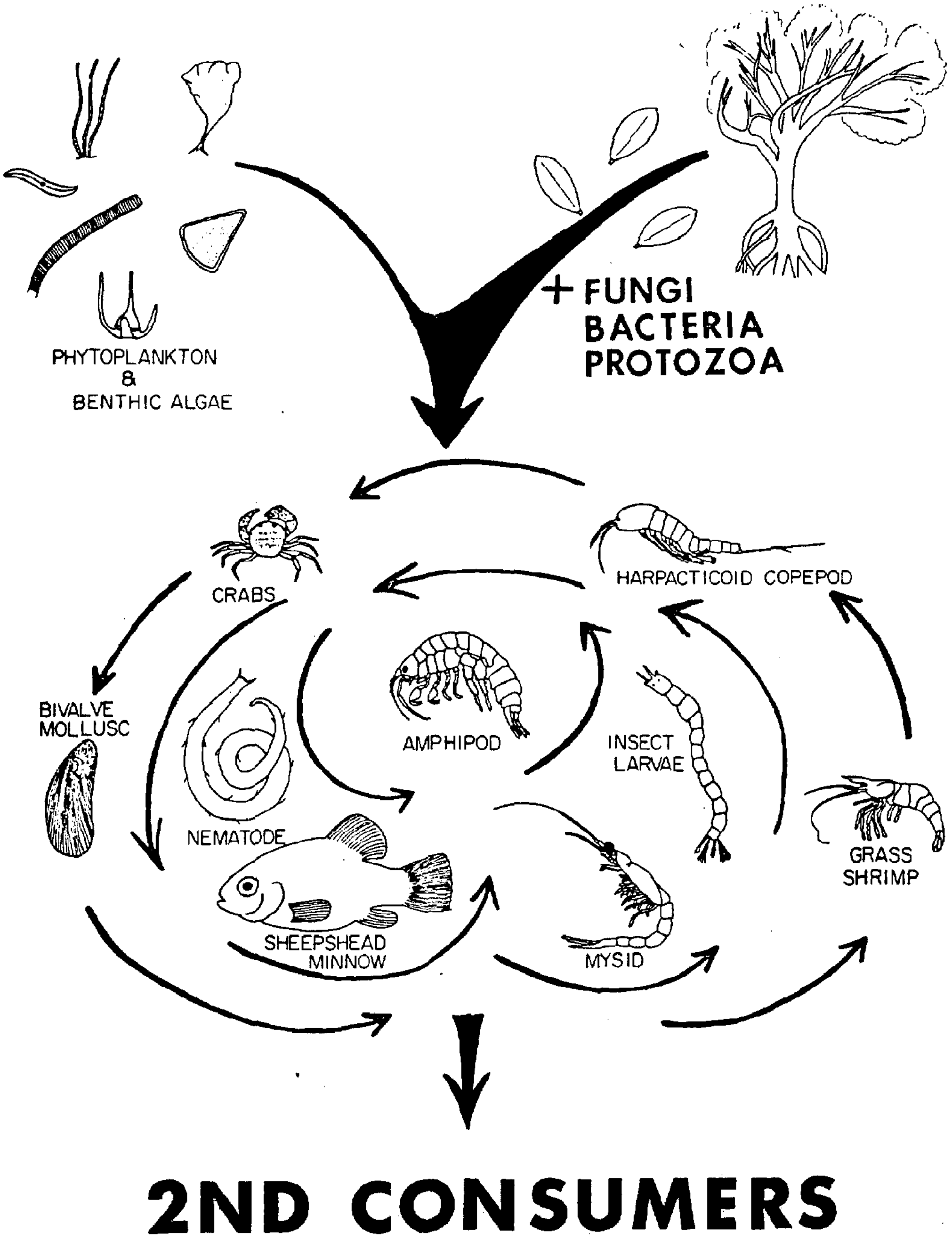
PHYTOPLANKTON
&
BENTHIC ALGAE
+ FUNGI
BACTERIA
PROTOZOA
CRABS
HARPACTICOID COPEPOD
BIVALVE
MOLLUSC
AMPHIPOD
INSECT
LARVAE
NEMATODE
GRASS
SHRIMP
SHEEPSHEAD
MINNOW
MYSID
2ND CONSUMERS

Fig. 8. Diagram of the detritus-based food web. The omnivorous detritus consumers ingest small amounts of living algae along with large quantities of vascular plant, largely Rhizophora, detritus. Much detrital material recirculates in the form of fecal matter (Odum, 1970).

HUMAN USE AND DISTURBANCE

Morton (1965) summarized the commercial uses of Rhizophora mangle: tannins and dyes for several purposes; durable and water-resistant timber for residential and boat construction, for pilings, hogsheads, and fence posts; wood for high-grade charcoal production; and various medicinal uses, teas, and livestock feed supplements. Moldenke (1967) reported similar usages for Avicennia germinans; in addition, it produces an abundant nectar that results in a clear, white honey of some importance (Argo, 1963). Holdridge (1940) described the utilization of timber products from the Puerto Rican species.

Mangrove swamps, with their dense tangle of firmly implanted roots, greatly reduce hurricane damage (Davis, 1940a). Although many of the trees may be defoliated, killed, broken off, or even swept away en masse by severe storms (Craighead and Gilbert, 1962); the damage to the coast is certainly less than if the swamps had not been present. The transplantation of mangroves to Hawaii, mentioned above, was for the purpose of erosion prevention (Walsh, 1967). The slow, long-range accumulation of sediments, and peat production, and eventual land building is certainly to be considered another human value of mangrove swamps.

Florida mangrove swamps serve as nursery grounds for many animals species of economic importance--menhadden, black mullet, spotted sea trout, snook, tarpon, red drum, mangrove snapper, pompano, and pink shrimp (Allin, 1966b,Tabb and Yokel, 1968). Sports fishermen as well as commercial fishermen are interested in preserving the total area and the quality of the environment in order to maintain good catches of fish. Edible oysters growing on the bottoms of shallow bays or on the mangrove prop roots are also harvested in some places. Mattox (1949) calculated that about $5,000 worth of oysters were taken annually from the mangrove roots of Laguna Rincon in Puerto Rico. Large land crabs are collected for human consumption many places in the world; Feliciano (1962) estimated the market value of Cardisoma guanhumi in Puerto Rico to be $70,000 per year.

The value of the swamps also includes their attractiveness to tourists. The uniqueness of this part of Florida was the reason for creation of Everglades National Park. There are 99 species of aquatic and wading birds, most of which inhabit the mangrove edges of the park or the keys of Florida Bay, and numerous other interesting animals--alligators, crocodiles, manatees, otters. In 1965 Everglades National Park had 226,000 boaters, most of them fishermen, over 100,000 campers, picnickers, and bird-watchers (Allin, 1966a). These people came to enjoy the rich wildlife associated with mangroves or dependant upon conditions resulting from the mangrove swamps. Nowhere else in the United States can this wildlife be seen and enjoyed in its natural habitat.

The mangrove areas of Puerto Rico have been greatly modified by human activities. About one-third of the original mangrove area has been completely destroyed by overcutting, dredging and filling, garbage dumps, or housing developments (Holdridge, 1940; Wadsworth, 1959). These pressures, plus the rapid increase in domestic and industrial pollution, are considered to be very harmful to optimal utilization of the swamps for food production, tourism, and recreation in Puerto Rico (Federal Water Pollution Control Administration, 1968d).

Human activities in Florida have not yet done irreversible damage to the major mangrove areas and their biota, but only far-sighted planning and broadly-based conservation practices will prevent ill-advised "development", gradual attrition, or destruction by altering water-flow patterns. Some of the lessons learned from other estuarine areas, for example New England salt marshes, are applicable. It is not possible to destroy a portion of the mangrove swamp every year for decades and yet expect the ecological system to remain the same size and the components to flourish as before. Ecological theory says that reduction in size of a habitat reduces the number of species--the diversity--of the system. Although this reduction in diversity may not be apparent, or seem important, to the layman, reduced variety of components in a system usually leads to less stability of the whole system and often to a loss of important species. The slow destruction as agricultural and residential developers move southward in Florida is serious. Even more serious is the potential for quick and perhaps permanent destruction resulting from mismanagement of the fresh-water drainage from the Florida Everglades. It is this water at the right season and of sufficient volume that has permitted the magnificent mangrove association to develop. Tabb (1963) has thoroughly documented the effects of this mismanagement of water in the Everglades and Tabb and Yokel (1968) warn against allowing damage to occur elsewhere. Reduced water volumes and improper timing during the last few decades have already caused great harm to the Everglades National Park and its fauna, especially the alligators and the beautiful spoonbills, egrets, ibis, herons, Everglades Kites, and bald eagles that help make this park famous. The threat to the mangrove trees from reduced freshwater flows is not so immediate because of their wide salinity tolerances, but some of the valuable commercial fisheries crops, such as the pink shrimp, may fail to mature in the Everglades estuary under changed conditions (Idyll, 1965b, c).

Few realistic appraisals have been made of the human values of mangrove swamps and, unfortunately, they have in the past been relegated, along with salt marshes, to the category of wastelands. Destruction by dredging and filling, by garbage dumps, or by housing developments, have usually been regarded as improvements. Numerous real values and benefits such as commercial products, shore protection, food production, recreation, and aesthetic beauty do accrue from the intact swamps, however, and it is unfortunate that these values may not be appreciated until they are lost.

RESEARCH NEEDS

This survey of present knowledge of mangrove swamps shows clearly that, although we know many details about different swamps, it is impossible to assess the overall structure and metabolism of any area anywhere in the world. We need more detailed information about zonation and succession and their causitive factors, about physiological adaptations to salinity and anaerobic sediments, about nutrient requirements and productivity of the trees and the attached algae, about the food webs, growth rates, and life tables of the mangrove animals, about the plankton and detritus of swamp waters and the relationships of the plankton to the benthic animals, about the final decomposition of organic matter by microbes, and about the human values of mangrove swamps. However, instead of continuing to learn in great detail different things in different parts of the world, we now need to bring together a few large teams of specialists who can do a thorough study of the structure and function of a few areas. The study of structure should include daily and seasonal measurements of physical and chemical factors in the air, water, and sediments, and population studies of plants and animals, including the plankton and the biota of the sediments. The study of function must include not only the metabolism of the individual organisms, but also the nutrition and metabolism of natural associations of organisms on the largest scale possible to avoid influencing the measurement being made. It is only by means of such large-scale studies and the synthesis of the results that we can begin to understand precisely how the whole system works, how it interacts with surrounding systems such as the land, the rivers, or the open sea, and how the system reacts to the various pressures which mankind exerts. Without such understanding mankind can quickly do serious damage to the mangrove ecosystem and unknowingly lose a valuable resource.

Chapter B-2

CORAL REEFS

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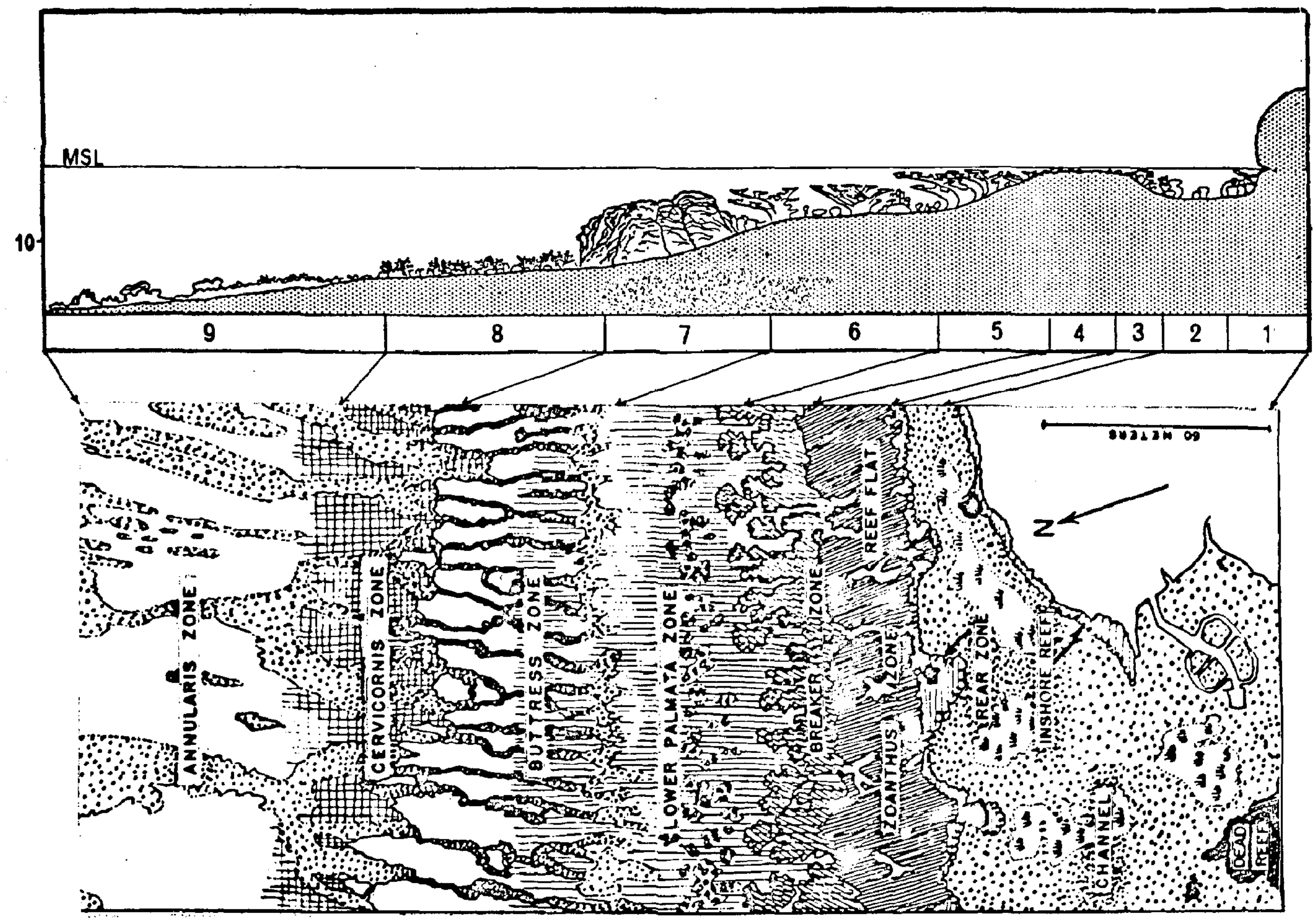
INTRODUCTION

Coral reefs are tropical shallow water ecosystems (Fig. 1) growing on their own limestone substratum and requiring bright light, stable high salinity, and temperatures above 70° F. Reef-building plants and animals continuously remove calcium and carbonate ions from seawater to produce skeletons which are incorporated into the limestone base. Attached to this substratum, crawling upon it, hidden within it, or swimming in close proximity are myriad creatures of bizarre color, form, and behavioral adaptation (Fig . 2). Diverse and ornate populations make coral reefs the most esthetically pleasing of underwater communities. The unusual physical structures and complexities of biological interaction have no rivals among the other coastal systems.

The principal reef builders of the present geologic era are the hermatypic corals. These corals contain, in the cells of the inner layer (Fig. 3) microscopic unicellular algae called zooxanthellae whose photosynthesis contributes to food and skeletal formation. Other important reef builders are some red and green algae which also produce carbonate skeletons. The most important of these are the encrusting red algae such as Porolithon (Fig. 4) which were highly important in reef building during the geologic past and persist as dominants in wave-swept buttress zones of many present day reefs (Fig. 5). Non-hermatypic corals occur in deeper, darker waters (Fig. 6).

Although there are many coral species which can grow and calcify in deep,cold waters, true coral reefs are not formed below a depth of 100 meters. Teichert (1958) reviews the occurrence and distribution of deepwater coral banks (See Fig. 12A).

The coral-algal symbiotic association aids the formation of massive reefs because of the unique advantages of the association. The symbiotic algae are protected in the tissues of the coral animals which are themselves protected by highly specialized cell products, the nematocysts (stinging organelles). The zooxanthellae are held up to the light by the basic structure of the coral, and further exposed in many corals whose polyps are extended from the corallum during the day (Wainwright, 1967). Figs. 7 and 8 show the coral heads' uptake of nutrients(Yonge,1931;Kawaguti,1953,1954).Algal photosynthesis and concomitant respiration by the coral are mutually beneficial. Algae typically produce oxygen and food contributions for the coral animal, whereas the coral releases carbon dioxide,phosphorus,nitrogen compounds,and other waste products used by algae to construct organic materials.With radioactive


MSL
10
9
8
7
6
5
4
3
2
1
60 METERS
Z
ANNULARIS ZONE
CERVICORNIS ZONE
BUTTRESS ZONE
LOWER PALMATA ZONE
BREAKER ZONE
REEF FLAT
ZOANTHUS ZONE
REAR ZONE
INSHORE REEF
CHANNEL
DEAD REEF

Region		Zone		Average Width (meters)	Average Depth (meters)
Back-reef region	1	Shore zone		1- 10	0.5- 3
	2	Lagoon or channel		10-300	2 -15
Reef crest	3	Rear zone		3- 10	1 - 3
	4	Reef flat		20- 50	0.5- 3
	5	*Palmata* zone	Upper (breaker)	0- 10	0.5- 3
	6		Lower	30- 50	3 - 6
	7	Buttress zone		40- 60	1 -10
Seaward slope or fore-reef	8	*Cervicornis* zone		30- 60	7 -15
	9	*Annularis* zone		>60	15

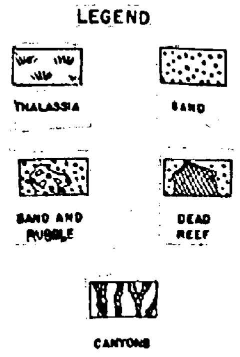

LEGEND
THALASSIA
SAND
SAND AND RUBBLE
DEAD REEF
CANYONS

Fig.1. A well developed Caribbean coral reef. Zonation of cross-sectional profile (top) and horizontal view (middle) are keyed at bottom. Zones are named for dominant coral species or general appearance. Buttress formation on this reef corresponds to algal ridge formation on wave-stressed Pacific reefs.(top Yonge, 1963a;others, Goreau, 1959 a).

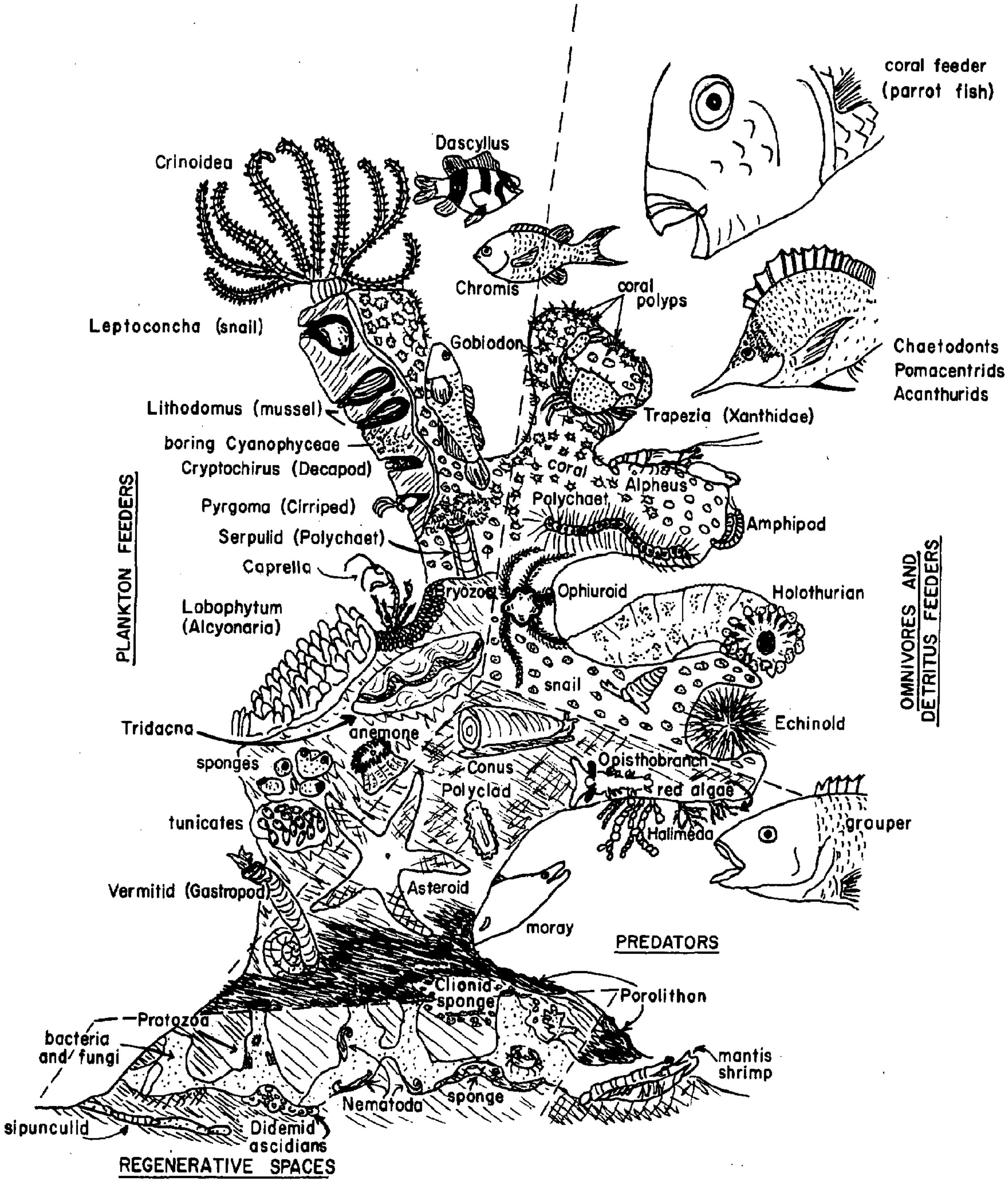
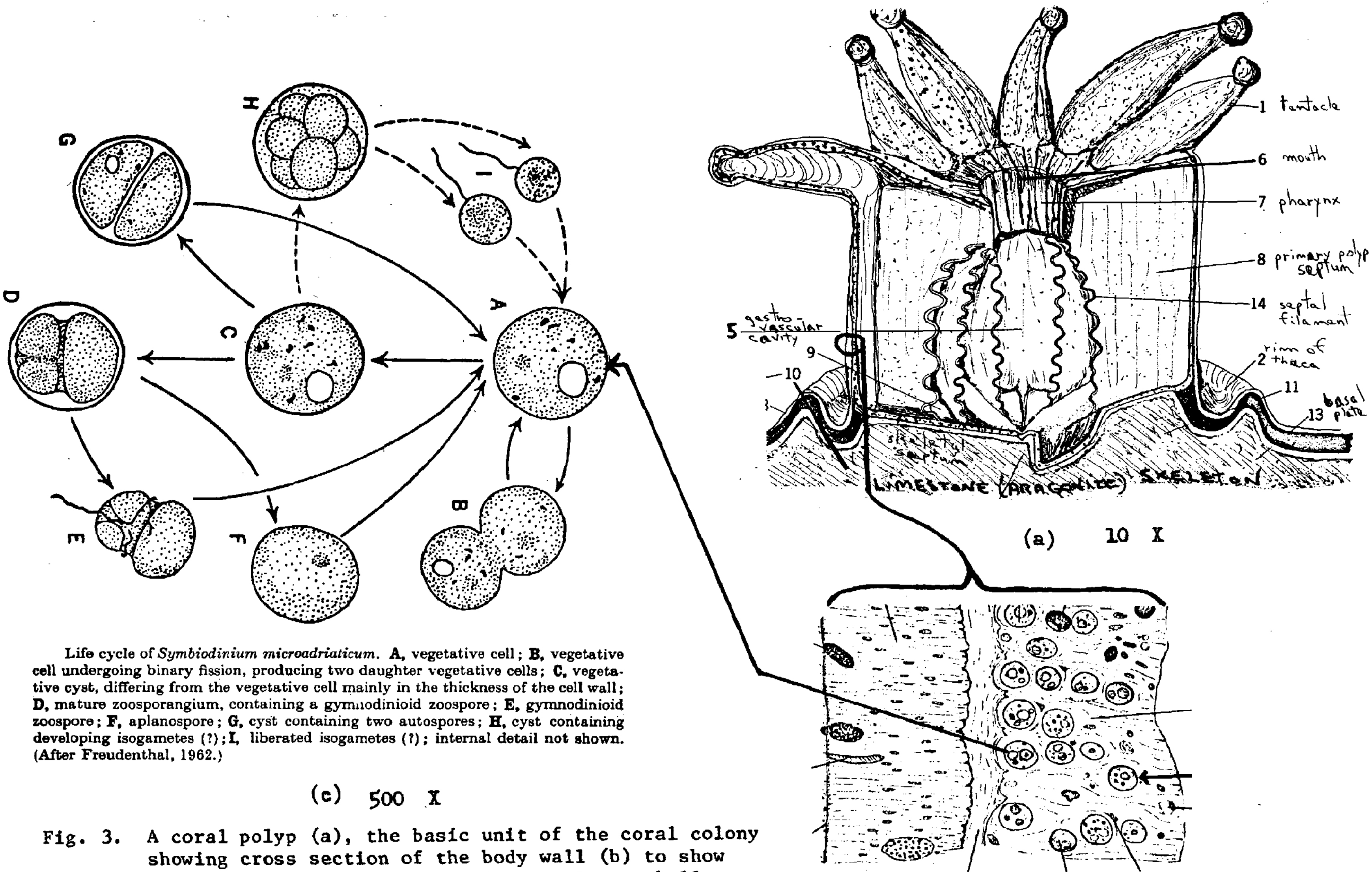

coral feeder (parrot fish)
Dascyllus
Crinoidea
Chromis
coral polyps
Leptoconcha (snail)
Gobiodon
Chaetodonts
Pomacentrids
Acanthurids
Lithodomus (mussel)
Trapezia (Xanthidae)
boring Cyanophyceae
Cryptochirus (Decapod)
Coral
Alpheus
Polychaet
Pyrgoma (Cirriped)
Amphipod
Serpulid (Polychaet)
Caprella
PLANKTON FEEDERS
Bryozoa
Ophiuroid
Holothurian
Lobophytum (Alcyonaria)
OMNIVORES AND DETRITUS FEEDERS
snail
Tridacna
anemone
Echinoid
sponges
Conus
Opisthobranch
Polyclad
red algae
tunicates
Halimeda
grouper
Vermitid (Gastropod)
Asteroid
moray
PREDATORS
Clionid sponge
Porolithon
Protozoa
bacteria and fungi
mantis shrimp
Nematoda
sponge
sipunculid
Didemnid ascidians
REGENERATIVE SPACES

Fig. 2. Conceptual diagram showing a collection of organisms in positions they might assume as part of the reef community. The segments of the community are arbitrarily partitioned to show some trophic relationships. (Modified after Gerlach, 1961).


A
B
C
D
E
F
G
H
I
1 tentacle
6 mouth
7 pharynx
8 primary polyp septum
14 septal filament
5 gastro-vascular cavity
9
10
3
2 rim of theca
11
13 basal plate
skeletal septum
LIMESTONE (ARAGONITE) SKELETON

Life cycle of *Symbiodinium microadriaticum*. **A**, vegetative cell; **B**, vegetative cell undergoing binary fission, producing two daughter vegetative cells; **C**, vegetative cyst, differing from the vegetative cell mainly in the thickness of the cell wall; **D**, mature zoosporangium, containing a gymnodinioid zoospore; **E**, gymnodinioid zoospore; **F**, aplanospore; **G**, cyst containing two autospores; **H**, cyst containing developing isogametes (?); **I**, liberated isogametes (?); internal detail not shown. (After Freudenthal, 1962.)

(a) 10 X

(b) 100 X

(c) 500 X

Fig. 3. A coral polyp (a), the basic unit of the coral colony showing cross section of the body wall (b) to show zooxanthellae in endodermal tissue. Zooxanthella enlarged (c) is shown with life cycle as it occurs in laboratory culture outside the host.

(a) Meglitsch (1967)
(b) Yonge (1931)
(c) Yonge (1963a)

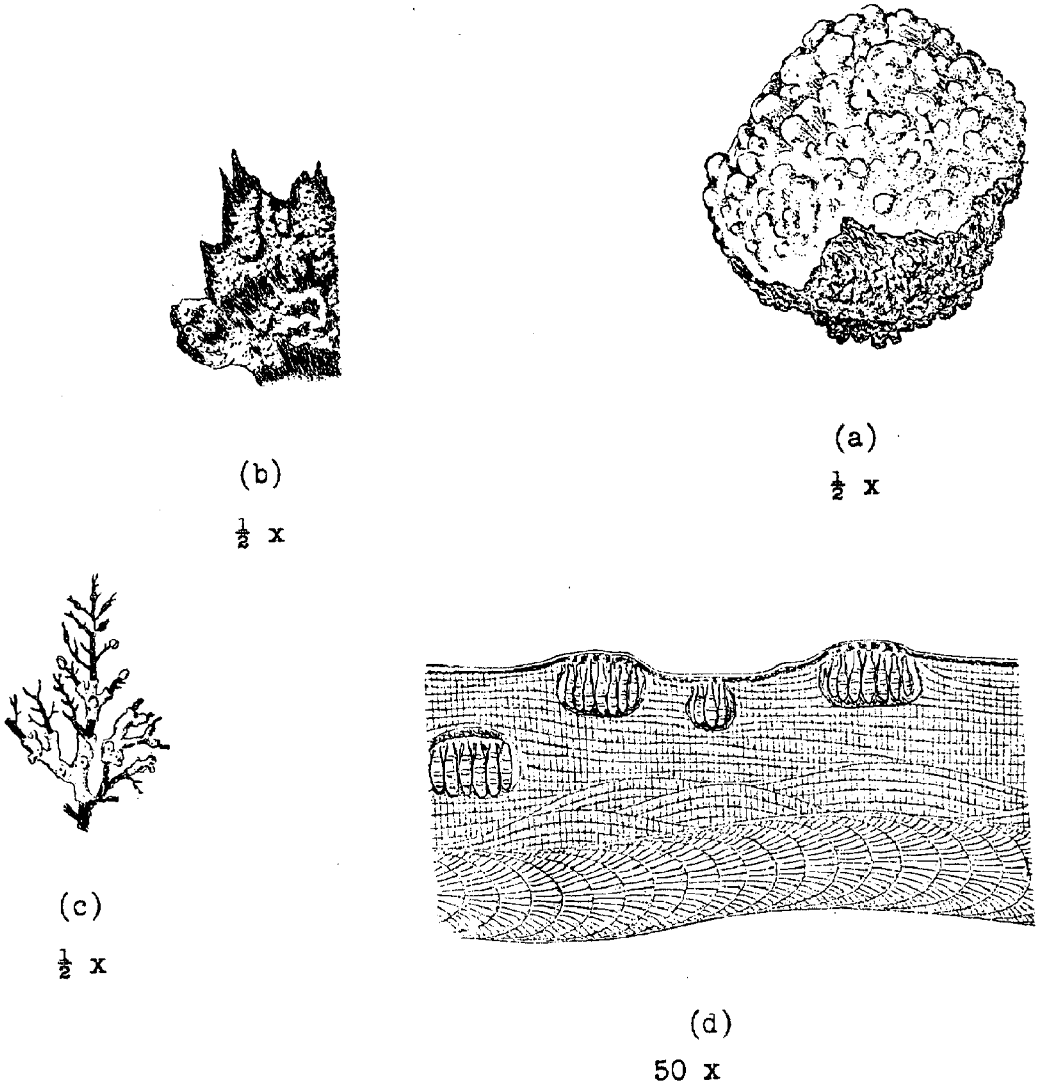
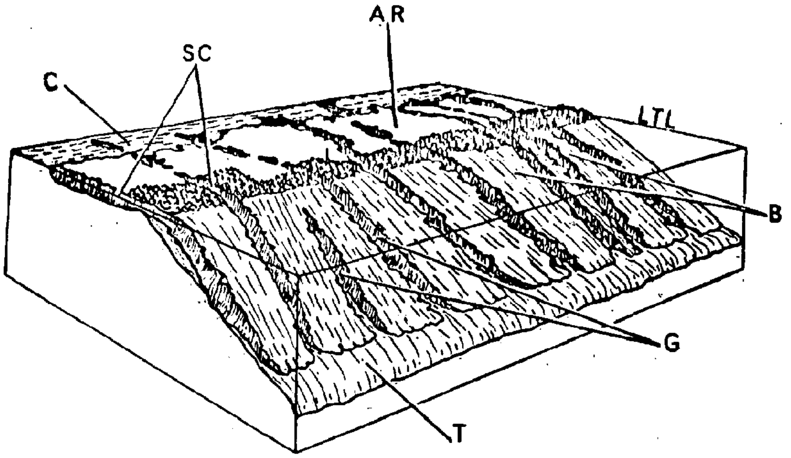
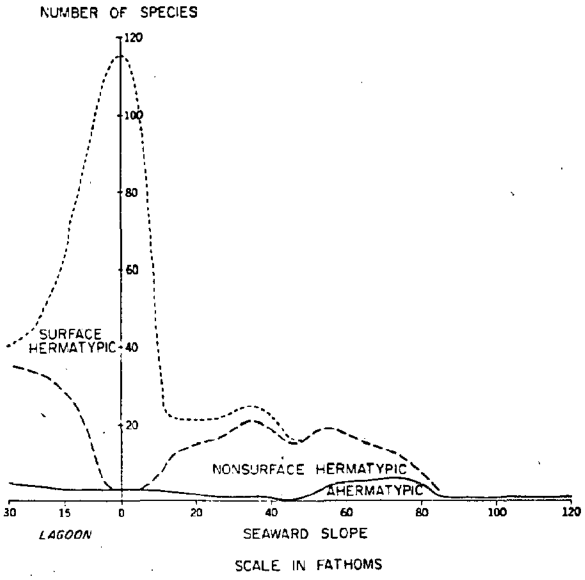


Fig. 4. *Porolithon* (*Lithothamnion*) spp. are important as producers of calcium carbonate and as cementing agents on coral reefs. (a) Shows thallus of an encrusting alga growing over a dead reef fragment, (b) and (c) show encrustations on other living algae, and (d) is a cross sectional view of the thallus to show reproductive structures (conceptacles) used for identification. Living tissue at the thallus surface leaves behind cell walls heavily calcified with high-magnesium calcite. (Oltmanns, 1904).



Generalized sketch of seaward face and top of reef on windward side of Bikini Atoll. AR, algal ridge; B, buttresses or spurs; C, coral of reef flat; G, grooves; LTL, low tide level; SC, surge channels; T, terrace (about 10 fathoms). (After Munk and Sargent, 1954.)

Fig. 5. A wave stressed seaward reef typical of Pacific reefs. (Yonge, 1963a).



—Bathymetric distribution of species at Bikini Atoll.

Fig. 6. Distribution of species with water depth over a Pacific atoll. The largest number of reef building species occupy shallowest waters. The ahermatypic corals thrive where light becomes limiting for hermatypes. Wells (1954).

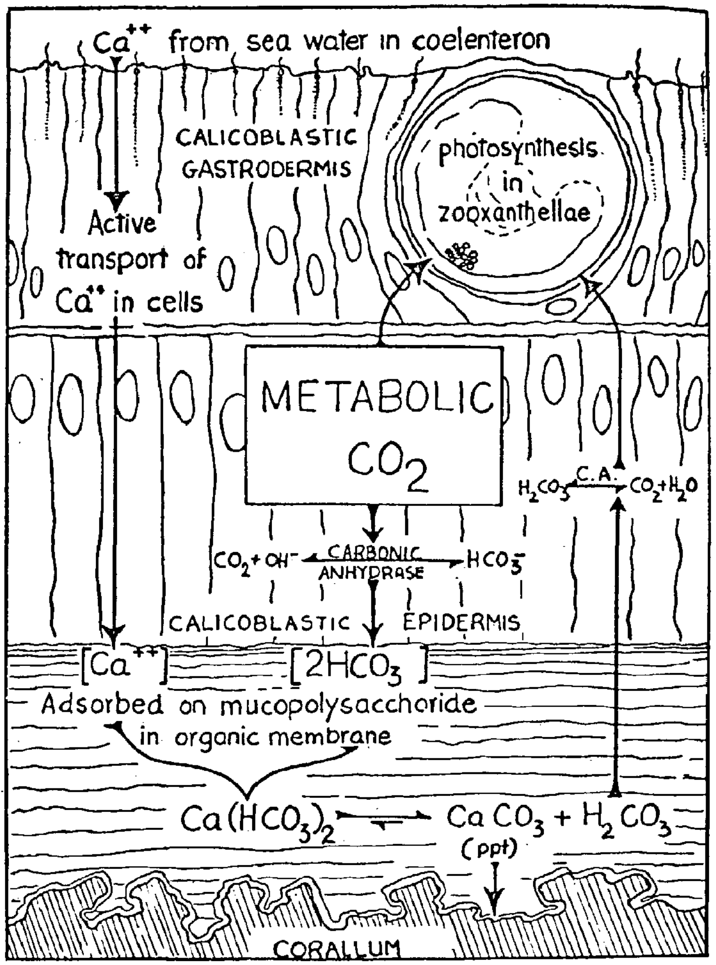
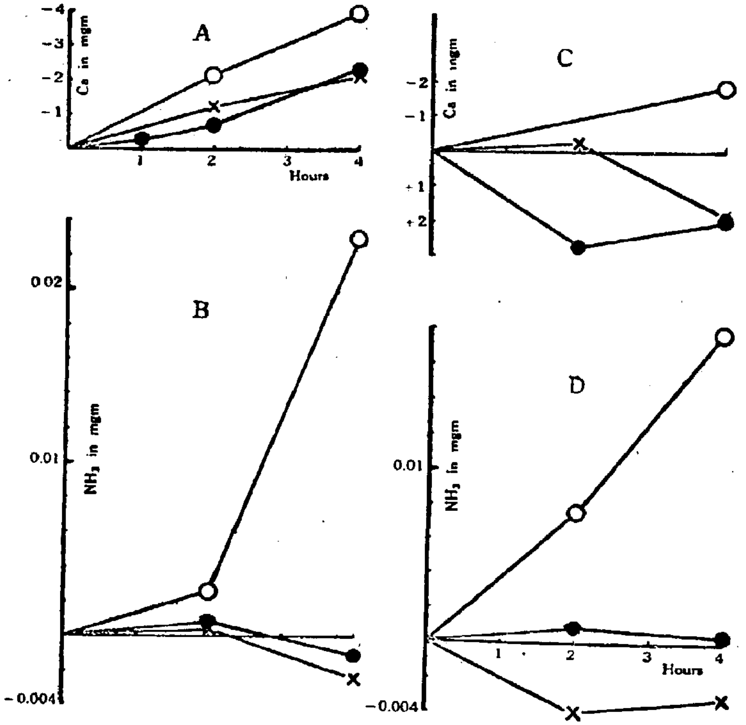

Ca++ from sea water in coelenteron
CALICOBLASTIC GASTRODERMIS
photosynthesis in zooxanthellae
Active transport of Ca++ in cells
METABOLIC CO2
H2CO3 C.A. CO2+H2O
CO2+OH- CARBONIC ANHYDRASE HCO3-
CALICOBLASTIC EPIDERMIS
[Ca++] [2HCO3]
Adsorbed on mucopolysaccharide in organic membrane
Ca(HCO3)2 CaCO3 + H2CO3
(ppt)
CORALLUM

Diagram (after Goreau, 1959a) showing possible pathways of calcium and carbonate during calcification in a reef-building coral. A diagrammatic cross-section of the calicoblastic body wall at the base of the polyp is shown but the parts are not drawn to scale. The coelenteron and the flagellated gastrodermis containing a zooxanthella are shown at the top of the figure, the calicoblastic epidermis is in the middle and the organic membrane with crystals of calcareous matter is at the bottom. The direction of growth is upward, i.e. calcium deposition is in a downward direction.

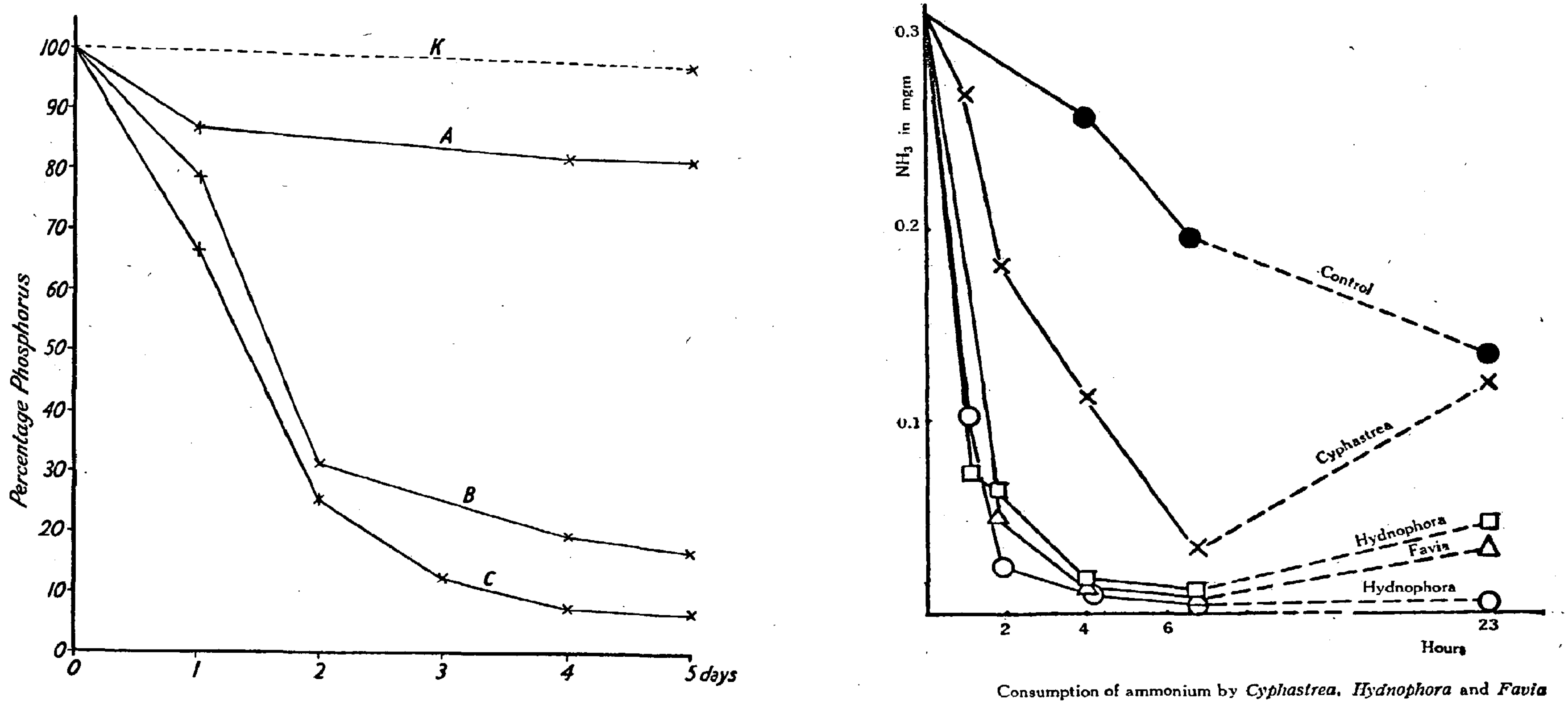
(a)



Ammonium (B, D) and calcium (A, C) metabolisms of *Balanophyllia*, *Psammocora* and *Oulastrea*, expressed by circles, dots and crosses respectively, in the light (A, B) and dark (C, D). Decreases or increases are calculated from the data given in Table I.

(b)

Fig. 7. Metabolic relationships of coral-algal symbiosis. (a) The possible relation between algal metabolism and calcification of the coral host. (b) The positive effect of light on coral metabolism of calcium and ammonium. Balanophyllia (open circles) has no zooxanthellae. (a) from Yonge, 1963a, (b) from Kawaguti (1953).



—Graph showing percentage change in phosphorus content of sea-water in jars containing corals. See Table III. A, *Psammocora*; B, *Porites*; C, *Favia*; K, control.

(a)

Consumption of ammonium by *Cyphastrea*, *Hydnophora* and *Favia* from the medium in which NH_3 is artificially increased by NH_4Cl. The experiment is carried out under the light of about 38,000 lux illumination for the first 4 hours and then in the dark. The total ammonium in the test medium is expressed in mgm. The initial volume of the test medium is 150 cc in each case. In *Cyphastrea* the specimen is killed by the end of 23 hours.

(b)

Fig 8. Coral metabolism studies in vitro. (a) shows uptake of phosphorus from surrounding waters, (b) shows uptake of ammonium by corals.
(a) from Yonge (1931), (b) from Kawaguti (1953).

tracers Muscatine (1967) showed that organic materials synthesized by the algae are released to the coral tissue, and Goreau (1959b, 1963) showed light accelerates calcification. Photosynthesis uses carbon dioxide raising the pH as diagrammed in Figure 7. Kawaguti (1944) found that the algal symbionts of corals and several other reef organisms were dinoflagellates, illustrated in Fig. 3. McLaughlin and Zahl (1959) have cultured these cells in vitro and described the life cycle.

Goreau and Wells (1967) list 48 species of reef building corals for Jamaican reefs, which probably approaches the maximum number of reef building species for the Caribbean region. Wells (1957) estimated that there were over 700 species of reef building corals among the typically more diverse Indo-Pacific reefs. A wide variety of coral skeletal forms exist, and these forms may be further diversified by morphological adaptations to waves and currents.

Fringing Reefs, Barrier Reefs, and Atolls

Coral reefs were classified generally by Darwin (1851) as a series of intergradations between initially formed fringing reefs, followed by development of barrier reefs, and finally atolls (Fig. 9). Reefs may arise either on continental footings or on islands which have arisen in the sea as a result of volcanic activity. Darwin presented the theory that coral reefs grow upward at a rate compensatory to the geological subsidence of volcanic platforms. A fringing reef, being the youngest geologically, may be found in many intergradations from newly colonized lava flows (Doty, 1967c) to established reefs (See Fig. 16). Barrier reefs sometimes occur many miles offshore (Fairbridge, 1950) often enclosing a distinct lagoon between themselves and a nearby land mass. Patch reefs may arise from this lagoon floor. An atoll is a coral reef in the form of a ring or semi-ring, delimiting a shallow (max. depth 350 ft) lagoon containing patch reef "knolls". Islands on atoll reefs are secondarily derived from reef sediments. The largest atoll (Kwajalein) is 66 miles long and 15 miles wide with a land surface area of 6.3 square miles (Wiens, 1962). The Florida (barrier) reef tract is about 200 miles long while Australia's great Barrier Reef extends over 1000 miles. Atlantic reefs are usually of the fringing type and are not as well developed as Pacific reefs. Three Caribbean atolls have been described (Stoddart, 1962a). Fringing, barrier and atoll reefs are distributed in specific patterns related to volcanism throughout the tropical Pacific and Indian Oceans (Darwin, 1851).

Cores from drilling (Fig. 10) have documented the geologic history of some reefs, supporting the Darwinian hypothesis of reef growth and basement subsidence. The relative rise in sea level from time to time in these records indicates that some reefs have existed for 100 million years or more.

Geographical Distribution

The distribution of reefs in most localities is determined by water clarity and other factors as presented in Fig. 11. The world distribution of reefs is illustrated in Figure 12. Northern limits of coral reef ecosystems

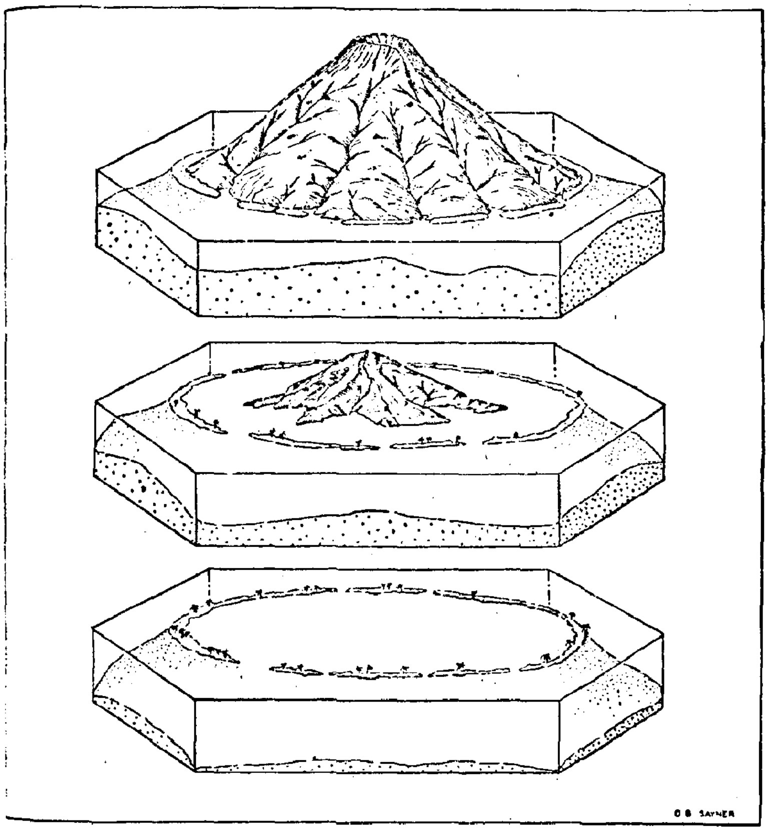
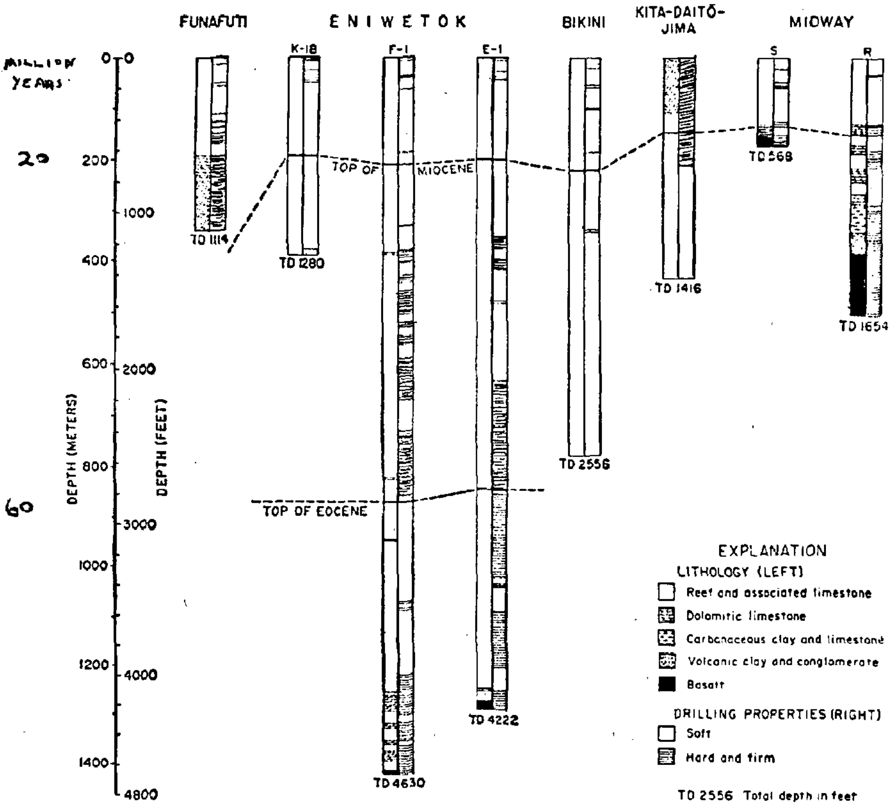


Fig. 9. Geological evolution of an atoll. According to the Darwinian hypothesis, fringing reefs grow around the edge of newly emerged volcanic rock (top). As volcanic platform subsides reef continues to grow upward enclosing a lagoon (middle). Finally, volcanic island disappears as reef continues to maintain itself at sea level. Maximum rate of reef growth is at outer edge. (Shepard, 1948).



Summary of results of deep drilling on atolls in the open Pacific Ocean. [After H. S. Ladd and S. O. Schlanger, *U.S. Geol. Survey Profess. Paper 260-Y* (1960), fig. 287]

Fig. 10. Results of rock corings used to determine geologic history of coral reefs. Basalt is volcanic rock upon which reefs originated. Presence of volcanic clay, conglomerate, and carbonaceous limestone indicates the conversion of reef limestone by freshwater (rains) as might occur during drops in sea level during glacial periods. The deeply lying basalt is evidence supporting Darwin's theory of platform subsidence and reef growth. (Ladd et al.,1967).

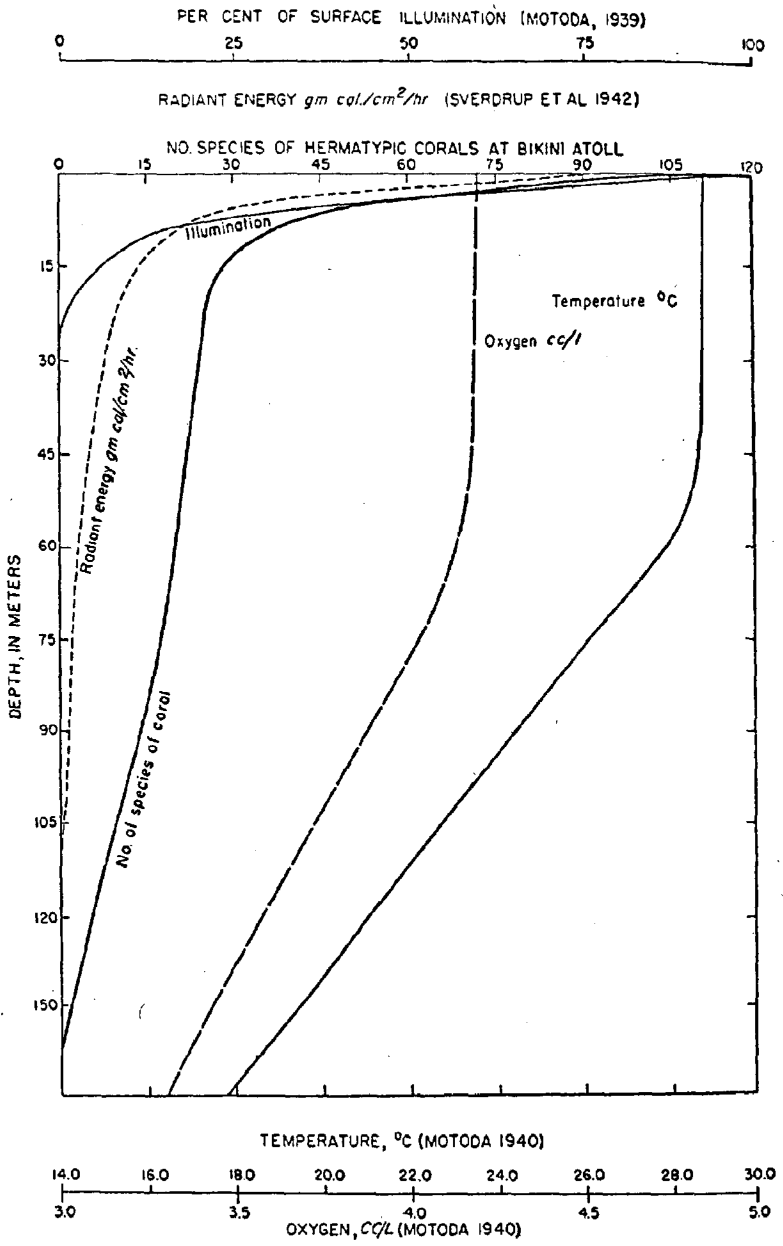
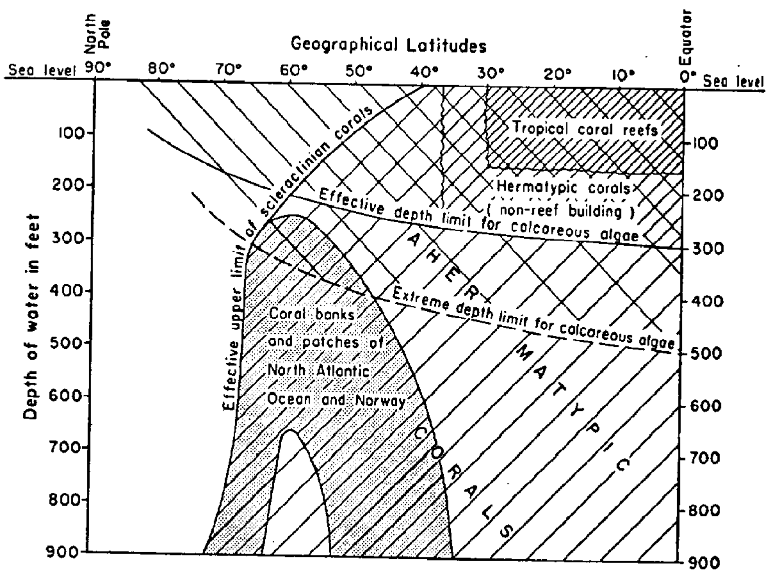
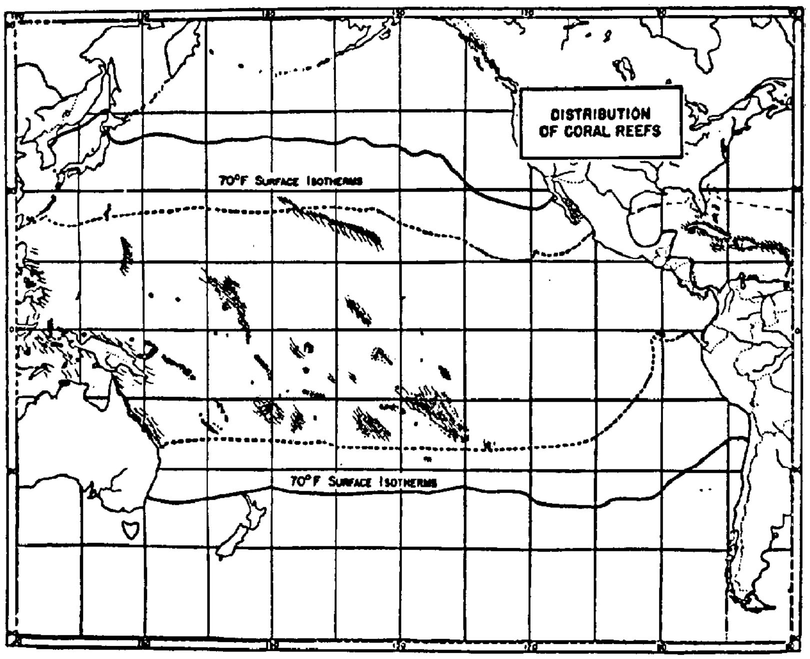


Fig. 11. **Graphic analysis of coral reef distribution according to depth, oxygen, temperature, illumination, and radiant energy. (Wells, 1957).**


North Pole
Geographical Latitudes
Equator
Sea level
90°
80°
70°
60°
50°
40°
30°
20°
10°
0°
Sea level
100
200
300
400
500
600
700
800
900
Depth of water in feet
Tropical coral reefs
Hermatypic corals (non-reef building)
Effective upper limit of scleractinian corals
Effective depth limit for calcareous algae
Extreme depth limit for calcareous algae
AHERMATYPIC CORALS
Coral banks and patches of North Atlantic Ocean and Norway

—Distribution of calcareous algae and of hermatypic and ahermatypic corals in different geographical latitudes on ocean floor to depth of 900 feet. Distribution of North Atlantic coral banks and patches also indicated.

Figure 12 a . World distribution of coral reefs (Teichert,1958).


DISTRIBUTION OF CORAL REEFS
70°F SURFACE ISOTHERMS
70°F SURFACE ISOTHERMS

.—A map of the Pacific Ocean showing the distribution of coral reefs within the summer and winter ranges of the 70° F. surface isotherms. Major coral reefs are illustrated by hatched areas; the solid lines illustrate the approximate locations of the 70° surface isotherms during the summer in each hemisphere, and the dotted lines represent the same surface isotherms during the winter in each hemisphere. (After J. W. Wells, 1957.)

Fig. 12b. World distribution of coral reefs (Helfrich and Townsley, 1965).

are apparently determined by winter temperature and associated temperate phenomena such as turbid, low salinity waters which move south along the Florida and Gulf coasts. Along the coast in the Gulf of Mexico reefs appear abruptly on islands near Tuxpan, Mexico off Cabo Rojo (Moore, 1959). Offshore a coral reef system was discovered only 100 miles from Galveston, Texas (T.E. Pulley, personal communication). Along the Atlantic coast a few patches of hermatypic corals exist as far north as Cape Lookout, North Carolina but reef systems are not formed (MacIntyre and Pilkey, 1969). On the west coast, waters are cool due to upwelling, and conditions amenable to the growth of reef builders are seldom encountered. Squires (1959) describes reefs found in the Gulf of California (Figure 13).

In the United States, only Florida and Hawaii possess coral reefs as coastal features. Well developed reefs occur around the coasts of Puerto Rico, Panama, and the U.S. Virgin Islands. Some of the world's best reefs are found in the tropical Pacific on islands of the U. S. Trust Territories, Guam, and American Samoa.

Fig. 14 is a detailed map of fringing reefs around St. John, U.S. Virgin Islands, a national park. Eniwetok and Bikini Atolls, U.S. Trust Territory of the Marshall Islands, are among the best studied coral reef areas as a result of geological, biological, and chemical studies carried out during U.S. testing of nuclear weapons at sites on these atolls. Hines (1962) provides a general account of these tests.

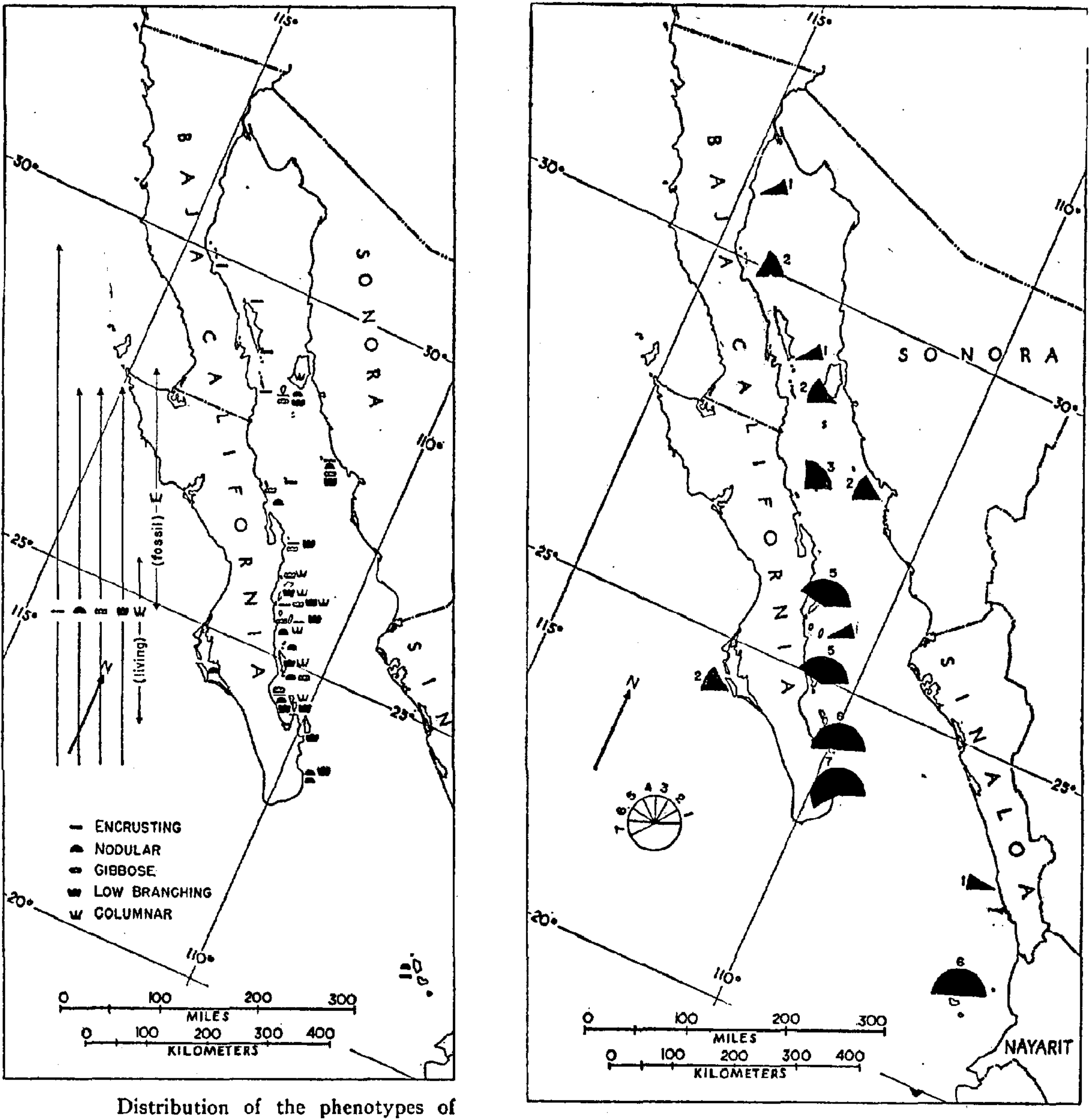
Figures 15 and 16 show variations in self grown limestone platforms of coral reefs of the Indo-Pacific region. Fig. 5 is an enlarged view of an algal ridge also shown in Fig. 16a. Distributions of coral species are also shown.

EXAMPLES

Small Reefs of Puerto Rico

Figure 17 locates patch reefs around the Commonwealth of Puerto Rico. The growth of reefs is favored on the dry southwest coast because the shores are protected from heavy winter waves and runoff and are favored by steady currents of clear water from the east. However, development of heavy industry with its associated addition of turbidity-inducing wastes to these ocean currents presently forms a serious threat to the reefs.

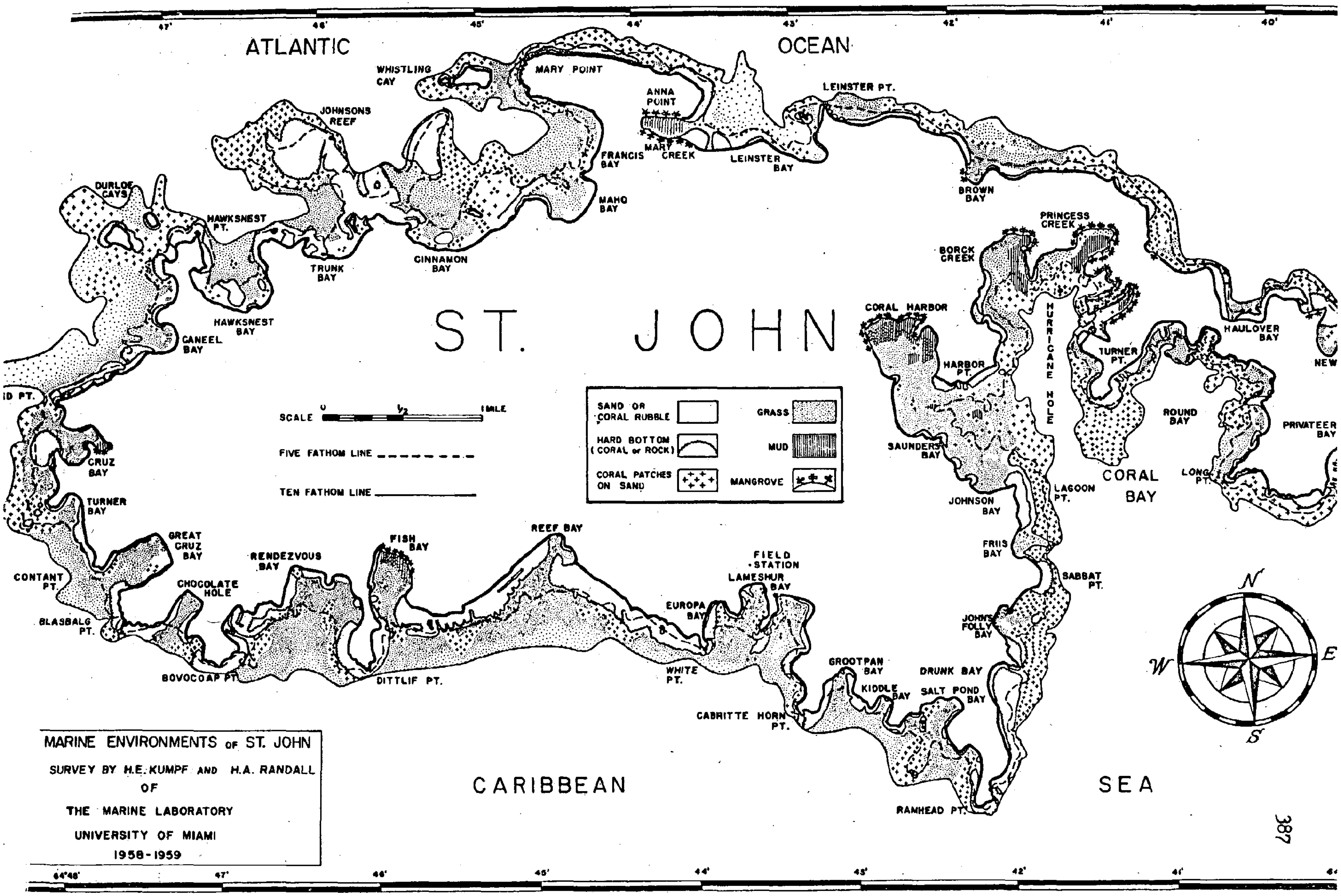
In Fig. 18 Glynn (1964) shows two animal associations found on these reefs. Changes in oxygen across these reefs was used to estimate photosynthetic productivity by Odum et al. (1959), as shown in Table 1 and Fig. 19. Beyers (1963), using pH changes, studied the diurnal balance of photosynthesis and respiration of isolated coral heads from these reefs (Fig. 20). The graphs show the daily respiration rates to be dependent on the previous day's photosynthesis. These results document high productivities as measured by day-night oxygen measurements on reef waters. Plant production of 29 g. per m^2 per day was recorded and respiration measurements indicated that the daily production was consumed the next night.


BAJA CALIFORNIA
SONORA
SINALOA
NAYARIT
30°
25°
20°
115°
110°
(living)
(fossil)
E
N
ENCRUSTING
NODULAR
GIBBOSE
LOW BRANCHING
COLUMNAR
MILES
0 100 200 300
KILOMETERS
0 100 200 300 400
1 2 3 4 5 6 7

Distribution of the phenotypes of *Porites californica* Verrill. Fossil distribution is shown only for the reef phenotype (symbols on land areas).

Numerical distribution of 13 shallow-water species representing the genera *Pocillopora*, *Pavona*, *Psammocora*, *Porites*, *Astrangia*, and *Tubastrea*. The size of the pie-shaped segment is proportional to the number of species (also given numerically) present at various localities.

Fig. 13. Reefs in the Gulf of California. These reefs are not well developed, and exist at the extreme northern limits of environmental tolerance for reef building corals. Structural and species diversity decrease northward up the Gulf. (Squires ,1959).


47'
46'
45'
44'
43'
42'
41'
40'
ATLANTIC
OCEAN
WHISTLING CAY
MARY POINT
JOHNSONS REEF
ANNA POINT
MARY CREEK
LEINSTER BAY
LEINSTER PT.
FRANCIS BAY
MAHO BAY
BROWN BAY
DURLOE CAYS
HAWKSNEST PT.
TRUNK BAY
CINNAMON BAY
PRINCESS CREEK
BORCK CREEK
HAWKSNEST BAY
CANEEL BAY
ST. JOHN
CORAL HARBOR
HARBOR PT.
HURRICANE HOLE
TURNER PT.
HAULOVER BAY
NEW
ID PT.
SCALE 0 ½ 1 MILE
FIVE FATHOM LINE
TEN FATHOM LINE
SAND OR CORAL RUBBLE
HARD BOTTOM (CORAL or ROCK)
CORAL PATCHES ON SAND
GRASS
MUD
MANGROVE
ROUND BAY
PRIVATEER BAY
SAUNDERS BAY
CORAL BAY
LONG PT.
CRUZ BAY
TURNER BAY
JOHNSON BAY
LAGOON PT.
GREAT CRUZ BAY
RENDEZVOUS BAY
FISH BAY
REEF BAY
FIELD STATION
LAMESHUR BAY
FRIIS BAY
SABBAT PT.
CONTANT PT.
CHOCOLATE HOLE
EUROPA BAY
JOHNS FOLLY BAY
BLASBALG PT.
N
W
E
S
BOVOCOAP PT.
DITTLIF PT.
WHITE PT.
GROOTPAN BAY
DRUNK BAY
KIDDLE BAY
SALT POND BAY
CABRITTE HORN PT.
MARINE ENVIRONMENTS OF ST. JOHN
SURVEY BY H.E. KUMPF AND H.A. RANDALL
OF
THE MARINE LABORATORY
UNIVERSITY OF MIAMI
1958-1959
CARIBBEAN
SEA
RAMHEAD PT.
64°48'
47'
46'
45'
44'
43'
42'
41'
64

Biotopic chart of St. John, U. S. Virgin Islands.

Fig. 14. Biotopic chart of St. John, Virgin Islands. Note reduced development of coastal features on eastern half of north shore subject to heavy winter wave action. (Kumpf and Randall, 1961).

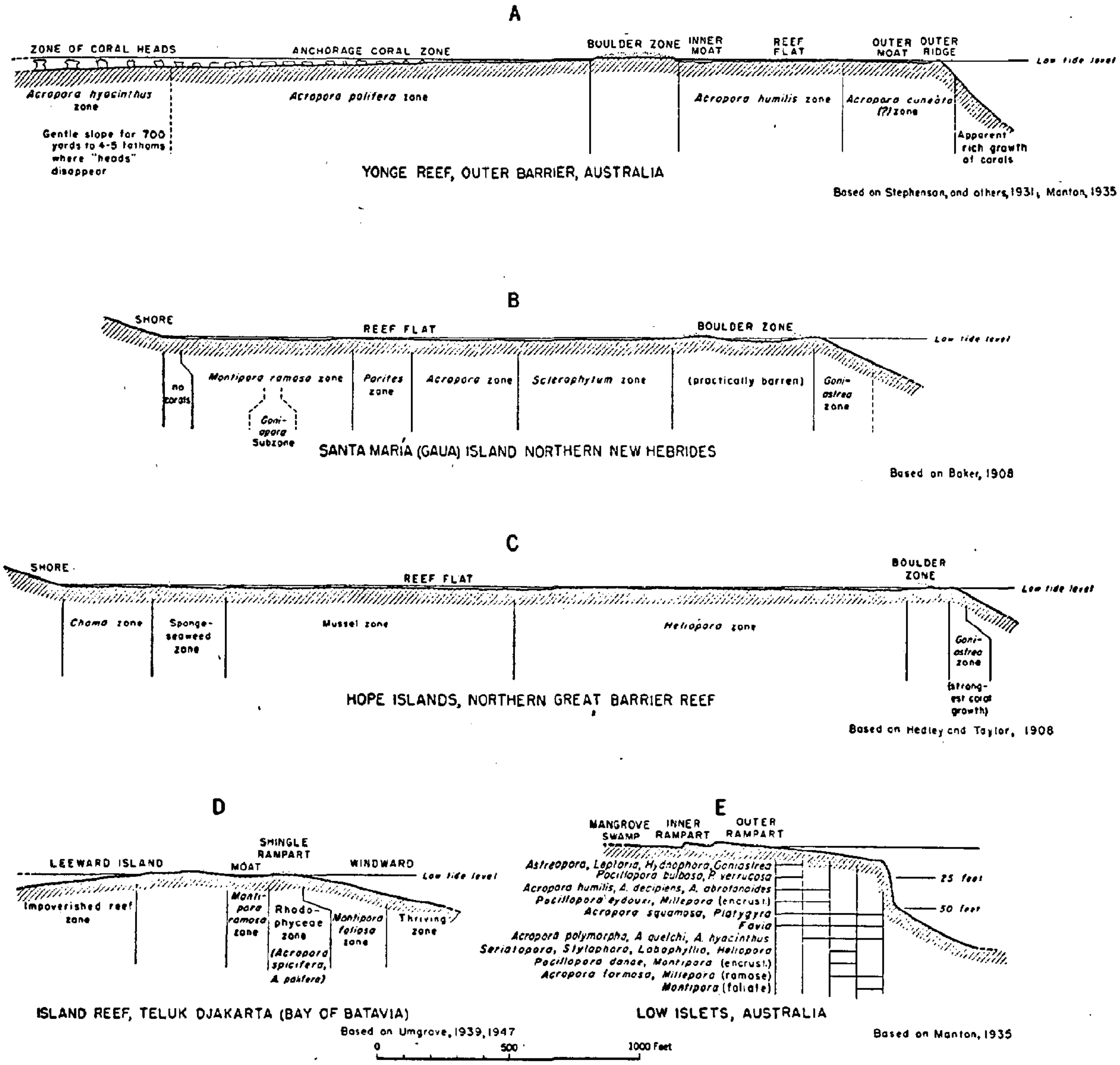

A
ZONE OF CORAL HEADS
ANCHORAGE CORAL ZONE
BOULDER ZONE
INNER MOAT
REEF FLAT
OUTER MOAT
OUTER RIDGE
Low tide level
Acropora hyacinthus zone
Acropora palifera zone
Acropora humilis zone
Acropora cuneata (?) zone
Gentle slope for 700 yards to 4-5 fathoms where "heads" disappear
Apparent rich growth of corals
YONGE REEF, OUTER BARRIER, AUSTRALIA
Based on Stephenson, and others, 1931; Manton, 1935
B
SHORE
REEF FLAT
BOULDER ZONE
Low tide level
no corals
Montipora ramosa zone
Goniopora Subzone
Porites zone
Acropora zone
Sclerophytum zone
(practically barren)
Goniastrea zone
SANTA MARÍA (GAUA) ISLAND NORTHERN NEW HEBRIDES
Based on Baker, 1908
C
SHORE
REEF FLAT
BOULDER ZONE
Low tide level
Chama zone
Sponge-seaweed zone
Mussel zone
Heliopora zone
Goniastrea zone
(strongest coral growth)
HOPE ISLANDS, NORTHERN GREAT BARRIER REEF
Based on Hedley and Taylor, 1908
D
LEEWARD ISLAND
SHINGLE RAMPART
MOAT
WINDWARD
Low tide level
Impoverished reef zone
Montipora ramosa zone
Rhodophyceae zone (Acropora spicifera, A. palifera)
Montipora foliosa zone
Thriving zone
ISLAND REEF, TELUK DJAKARTA (BAY OF BATAVIA)
Based on Umgrove, 1939, 1947
0
500
1000 Feet
E
MANGROVE SWAMP
INNER RAMPART
OUTER RAMPART
Astreopora, Leptoria, Hydnophora, Goniastrea
Pocillopora bulbosa, P. verrucosa
Acropora humilis, A. decipiens, A. abrotanoides
Pocillopora eydouxi, Millepora (encrust.)
Acropora squamosa, Platygyra
Favia
Acropora polymorpha, A. quelchi, A. hyacinthus
Seriatopora, Stylophora, Lobophyllia, Heliopora
Pocillopora danae, Montipora (encrust.)
Acropora formosa, Millepora (ramose)
Montipora (foliate)
25 feet
50 feet
LOW ISLETS, AUSTRALIA
Based on Manton, 1935

Fig. 15. Cross sections of windward Pacific reefs not showing development of algal buttress. Note differences in size, geomorphology, and coral species zonation. (Wells, 1954).

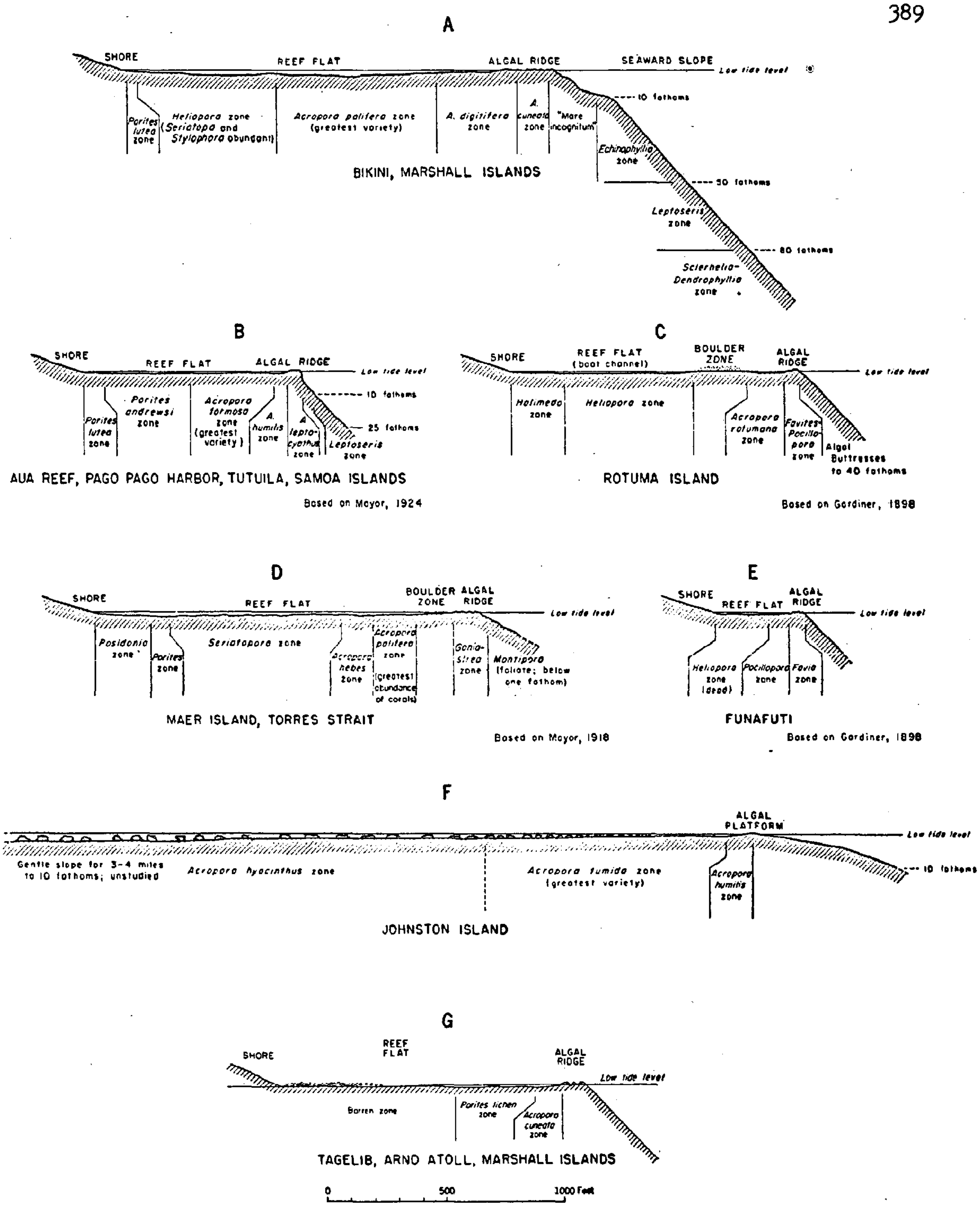

A
SHORE
REEF FLAT
ALGAL RIDGE
SEAWARD SLOPE
Low tide level
10 fathoms
Porites lutea zone
Heliopora zone (Seriatopa and Stylophora abundant)
Acropora palifera zone (greatest variety)
A. digitifera zone
A. cuneata zone
"Mare incognitum"
Echinophyllia zone
50 fathoms
Leptoseris zone
80 fathoms
Sclerhelia-Dendrophyllia zone
BIKINI, MARSHALL ISLANDS
B
SHORE
REEF FLAT
ALGAL RIDGE
Low tide level
10 fathoms
25 fathoms
Porites lutea zone
Porites andrewsi zone
Acropora formosa zone (greatest variety)
A. humilis zone
A. leptocyathus zone
Leptoseris zone
AUA REEF, PAGO PAGO HARBOR, TUTUILA, SAMOA ISLANDS
Based on Mayor, 1924
C
SHORE
REEF FLAT (boat channel)
BOULDER ZONE
ALGAL RIDGE
Low tide level
Halimeda zone
Heliopora zone
Acropora rotumana zone
Favites-Pocillopora zone
Algal Buttresses to 40 fathoms
ROTUMA ISLAND
Based on Gardiner, 1898
D
SHORE
REEF FLAT
BOULDER ZONE
ALGAL RIDGE
Low tide level
Posidonia zone
Porites zone
Seriatopora zone
Acropora hebes zone
Acropora palifera zone (greatest abundance of corals)
Goniastrea zone
Montipora (foliate; below one fathom)
MAER ISLAND, TORRES STRAIT
Based on Mayor, 1918
E
SHORE
REEF FLAT
ALGAL RIDGE
Low tide level
Heliopora zone (dead)
Pocillopora zone
Favia zone
FUNAFUTI
Based on Gardiner, 1898
F
ALGAL PLATFORM
Low tide level
Gentle slope for 3-4 miles to 10 fathoms; unstudied
Acropora hyacinthus zone
Acropora tumida zone (greatest variety)
Acropora humilis zone
10 fathoms
JOHNSTON ISLAND
G
SHORE
REEF FLAT
ALGAL RIDGE
Low tide level
Barren zone
Porites lichen zone
Acropora cuneata zone
TAGELIB, ARNO ATOLL, MARSHALL ISLANDS
0
500
1000 Feet

Fig. 16. Cross sections of windward Pacific reefs showing development of algal buttress zone as in Fig. 5. (Wells, 1954).

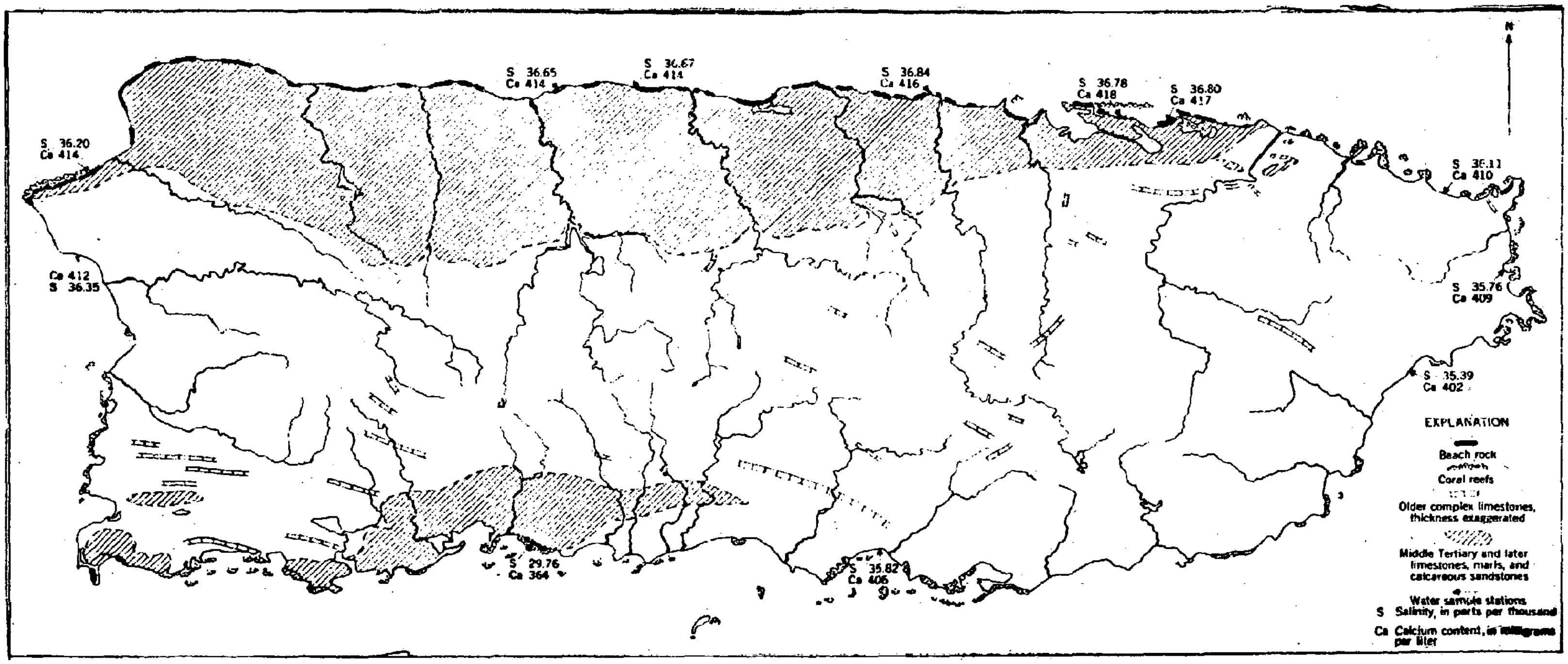

N
S 36.20
Ca 414
Ca 412
S 36.35
S 36.65
Ca 414
S 36.67
Ca 414
S 36.84
Ca 416
S 36.78
Ca 418
S 36.80
Ca 417
S 36.11
Ca 410
S 35.76
Ca 409
S 35.39
Ca 402
S 29.76
Ca 364
S 35.82
Ca 406
EXPLANATION
Beach rock
Coral reefs
Older complex limestones, thickness exaggerated
Middle Tertiary and later limestones, marls, and calcareous sandstones
Water sample stations
S Salinity, in parts per thousand
Ca Calcium content, in milligrams per liter

Fig. 17. Distribution of beachrock, coral reefs, and limestone in Puerto Rico. Coral colonies that do not reach the tide level are not shown, although several offshore reefs exist. Note reduction of coral reefs on wave stressed north shore. (Kaye, 1959).

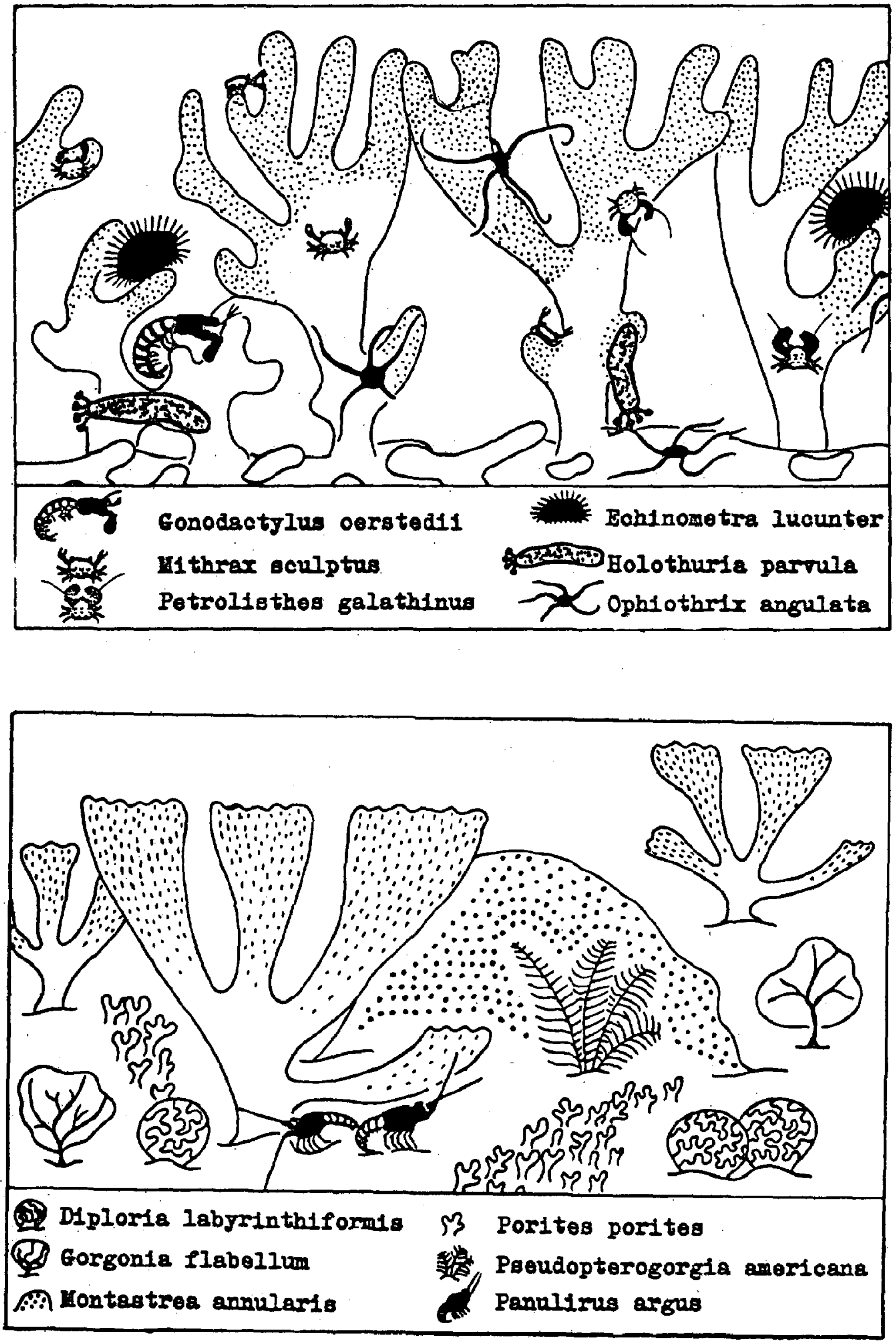

Gonodactylus oerstedii
Mithrax sculptus
Petrolisthes galathinus
Echinometra lucunter
Holothuria parvula
Ophiothrix angulata
Diploria labyrinthiformis
Gorgonia flabellum
Montastrea annularis
Porites porites
Pseudopterogorgia americana
Panulirus argus

Fig. 18. Conceptual presentation of two common reef community types in Puerto Rico. Large branching coral species in upper diagram is Porites furcata, in lower diagram, Acropora palmata. (Glynn, 1964).

Table 1. Oxygen metabolism measurements on Puerto Rican coral reefs and adjacent environments (Odum et al., 1959).

Oxygen Metabolism (grams/m²) in the Waters of Southwestern Puerto Rico
(Pcn=net daytime community photosynthesis per hour; R=night time community respiration per hour: Pg=net photosynthesis per day with night R added; R_{24} = 24 hour community respiration based on night R.

Community and location	Depth (m)	Current (m/min)	Temp. (°C)	Date	Time	Method used key below	P_{cn}	R	P_g	R_{24}
East La Gata Reef,				Feb. 27	1310	AF	1.75	.....	.....	.....
Porites reef	0.26	7.6	27.5	1958	1335	AF	2.8	.....	.....	.....
La Gata, *Thalassia* bed		7.3	27.5	Feb. 27 1958	1100	AF	2.8	.....	.....	.....
La Gata Reef, *Porites* and *Thalassia*	0.3	slight	25–28	Feb. 18 1958	24 hrs.	BC	1.8+	1.8+	8.6+	11.3+
West La Gata Reef, *Thalassia*	0.26	6.4	27–28	Feb. 28 1958	1100	AF	2.6	.....	.....	....
Margarita Reef, *Porites* carpet	0.23	0–9	25–28	Feb. 25 1958	24 hrs.	A	1.4	0.5–4	44	....
Isla Magueyes, southern shore, *Porites* and *Thalassia*	0.3	0–3	25–29	Feb. 17 1958	24 hrs.	BC	0.32+	0.75+	12+	18+
La Media Luna, ***Millepora***, 18m; ***Acropora*** and *Porites* 65m	0.28–3	5–8	28–30	June 12 1959	24 hrs.	AC	2.0	1.21	38.4+	29+
Las Palmas, *Thalassia*	0.3	1.8	25–28	Feb. 28 1958	1237	AF	1.33	.....	.....	.....
Channel north of Isla Magueyes, *Thalassia*	1.2–1.5	4.2	26–28	Feb. 13 1958	24 hrs.	BG	0.50	0.52	10.5	12.5
	1.2–1.5	...	25–28	Mar. 1 1958	24 hrs.	BG	0.60	0.45	11.0	12.5
Enrique Reef, Millepora Thalassia Zoanthus, Dictyota, Porites	0.1–0.6	6.4	27–29	Mar. 12 1958	24 hrs.	A	2.0	0.90	20.0	17.3
El Mario Reef	0.39	4–8		May 29 1959	24 hrs.	AF	1.6	1.5	39	36
Bahia Fosforescente, Total Bay	4			Jan. 24 1957	24 hrs.	B	0.08	0.29	5.6	7.7
Plankton only	4	....		Jan. 24 1957	24 hrs.	D (Table 2)	0.06	0.09	1.4	2.3
Thalassia bed	.....	....		Feb. 12 1958	24 hrs.	BC	0.85+	0.75+	15+	18+
Thalassia bed	.....	....		Mar. 13 1958	24 hrs.	BC	.....	.....	5+	5+
Total Bay	4	....		Mar. 13 1958	24 hrs.	See text	.....	.....	<48	<48
						C	.....	.....	8.8	7.7
Plankton only	4	....		June 1 1959	24 hrs.	D	–0.18	0.29	1.4	6.9

A. Upstream-downstream change
B. Diurnal curve—single water mass method
C. Since there is some admixture of water from other areas, this estimate is minimal
D. Dark and light bottles.
E. Data over a 24 hour period
F. With standard diffusion correction
G. Upstream-downstream measurements were similar and averaged.

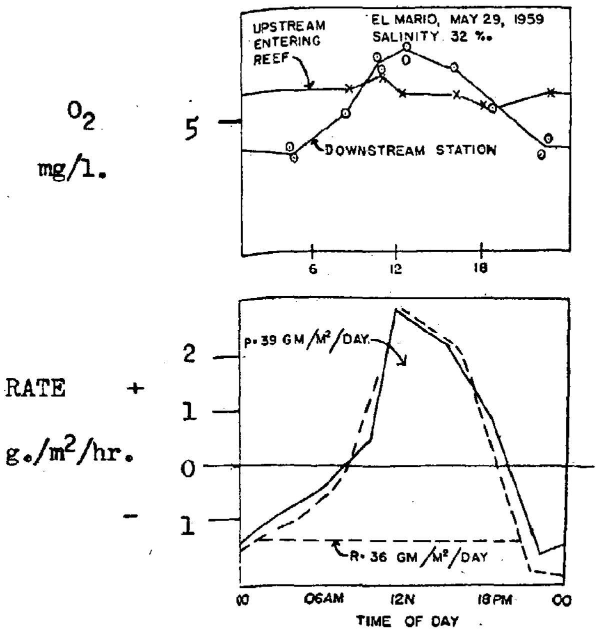
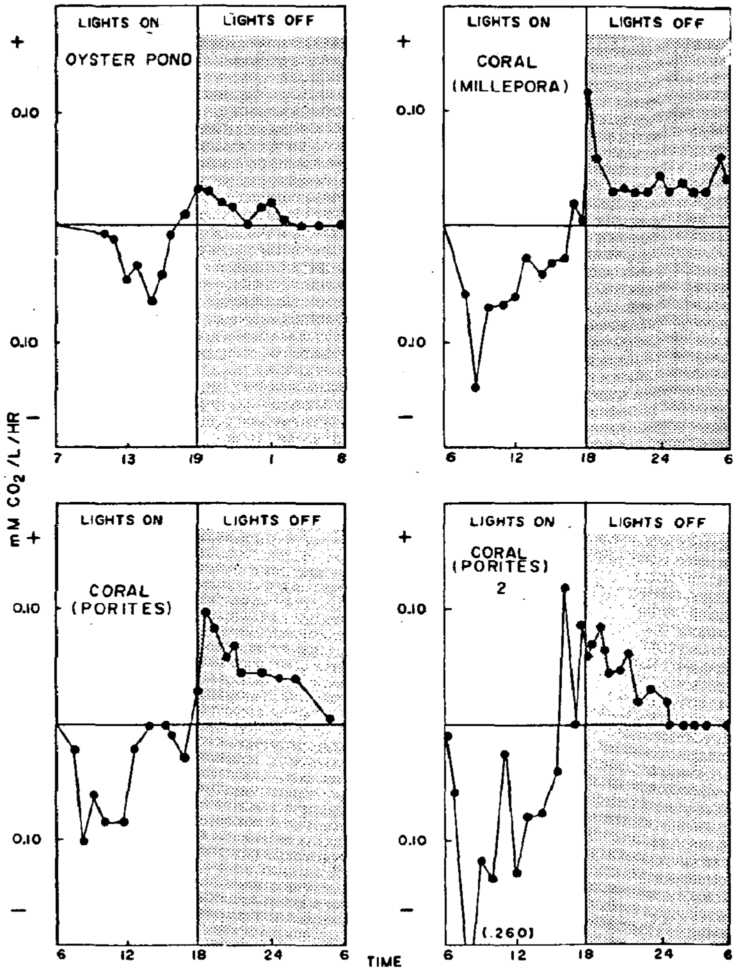


Fig. 19. Diurnal productivity measurements on a Puerto Rican coral reef, measured as change in dissolved oxygen of reef waters. Production during daytime (P) almost equals night-time consumption (R). (Odum et al., 1959).



Diurnal rates of carbon dioxide uptake and release during net photosynthesis and night-time respiration in an oyster pond microcosm and in three small, isolated coral heads.

Fig. 20. Productivity measurements on individual reef corals by measurement of carbon dioxide. The corals consume more CO_2 than they produce due to metabolic requirements of symbiotic algae. (Beyers, 1963).

Florida and Nearby Reefs

Fringing the curve from Miami southwestward to Key West and several miles to the east of the Key West Highway lies a barrier reef. East of it, in the Florida Strait, flows the Gulf stream (Figs. 21, 22,23). Further to the east lie the Bahama Banks with their numerous islands and extensive reef flats.

The Florida reef tract extends some 200 miles ending in a few small reef islands, the Marquesas Keys and the Dry Tortugas. The lagoonal waters to the west of the Florida reef alternate with islands having occasional patch reefs. The first 30 miles of coral reefs from Key Largo south are preserved as the John Pennekamp State Park. The Marquesas Keys are a National Wildlife Refuge, while the Dry Tortugas are preserved as a National Monument. Like most Atlantic coral reefs, the Florida tract is mainly several feet below the water surface at low tide, contrasting with Pacific reefs which are generally at the surface at lowest tides. This could be explained by a recent rise in sea level with coral growth being inadequate to keep pace with the rising waters although conclusive evidence is not available. The lower nutrient levels of the Atlantic Ocean as compared to the Pacific may be a contributing factor (Sverdrup et al, 1942).

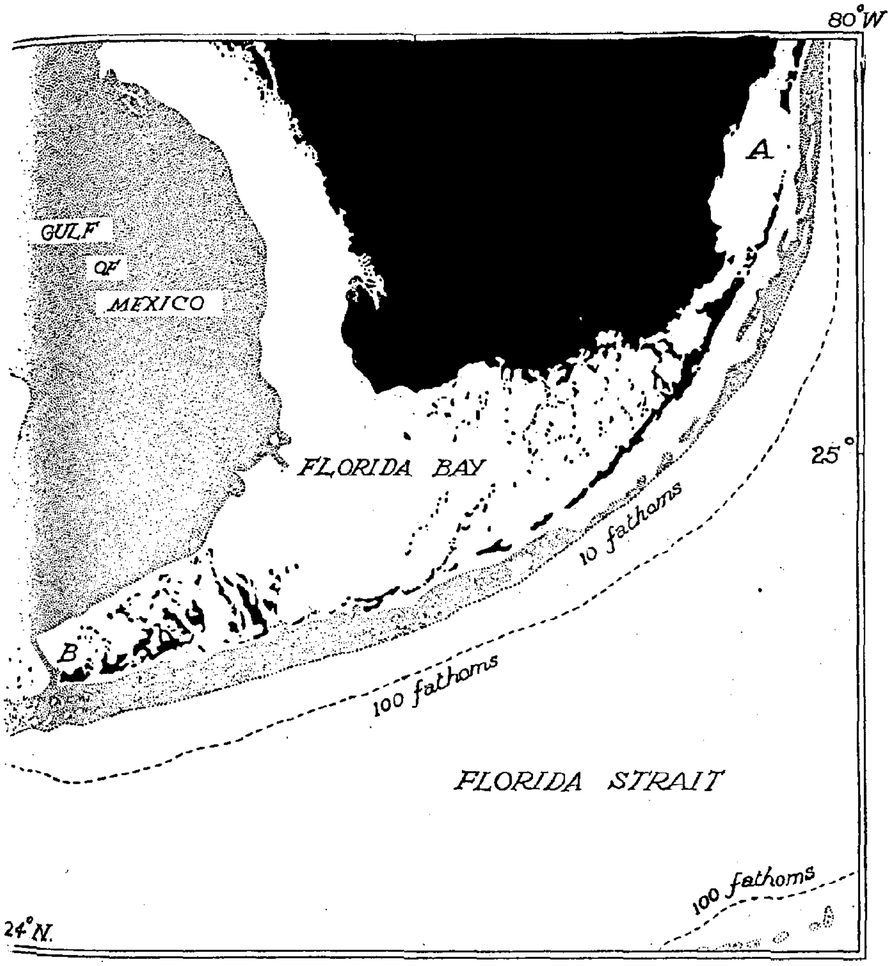
Fig. 24 depicts a poorly developed reef occurring toward the northward limits of reef formation in Florida. Graded changes occur in a southerly direction as conditions for reef formation improve. The well developed reef described by Goreau (1959) and depicted in Fig. 1 shows characteristic Atlantic reef structure. Storr (1964a)studying reefs in the Bahamas at Abaco Island across from Florida listed the following zonation from shore to deep water: urchins and encrusting algae, Porites corals, Acropora corals, Alcyonarian corals (sea fans), and massive Montastrea corals (Fig. 24).

Fig. 25 gives a cross sectional diagram of the Florida reef tract and shows the distribution of different types of calcareous sediments, mainly derived from skeletons in the several reef zones.

Individual reef corals from the Florida Keys studied by Kanwisher and Wainwright (1967) had high ratios of net photosynthesis to dark respiration, as listed in Table 2. Their results showed that the zooxanthellae photosynthesizing within the coral tissues cause the corals to be among the most productive organisms in the world. Table 3 is a study of metabolism in free water and measured with bottles filled with water from near reefs at the northern extremity of the Florida tract (Fig. 22). The mean of 3.6 g dry matter per m^2 per day is much lower than values found for more highly developed reef areas. Considerable destruction of reefs occurs with hurricanes (Shinn, 1963).

Eniwetok and Bikini Atolls

Much work has been done on the biology and geology of Pacific reefs, particularly in conjunction with nuclear weapons testing carried out on Eniwetok and Bikini Atolls. These reefs are some of the best developed and most diverse of marine communities, where structural and functional adaptations reach utmost complexity. Figs. 5 ,6,9 , and 26, 27 illustrate reef morphology (Emery et al., 1954; Ladd et al. 1950; Tracey et al., 1948).


80°W
A
GULF
OF
MEXICO
FLORIDA BAY
25°
10 fathoms
B
100 fathoms
FLORIDA STRAIT
100 fathoms
24°N.

A map of the Florida Key region. Land is shown in black, and the shallow inshore water (less than 3 fathoms deep) in white. Following this, the water between 3 and 10 fathoms is closely dotted, after which the deeper water (10–100 fathoms and over 100 fathoms) is again white, but the 100-fathom line is indicated.

Fig. 21. General view of Florida reef tract. The Dry Tortugas and Marquesas Keys lie farther westward, and are not shown. (Stephenson and Stephenson, 1950).

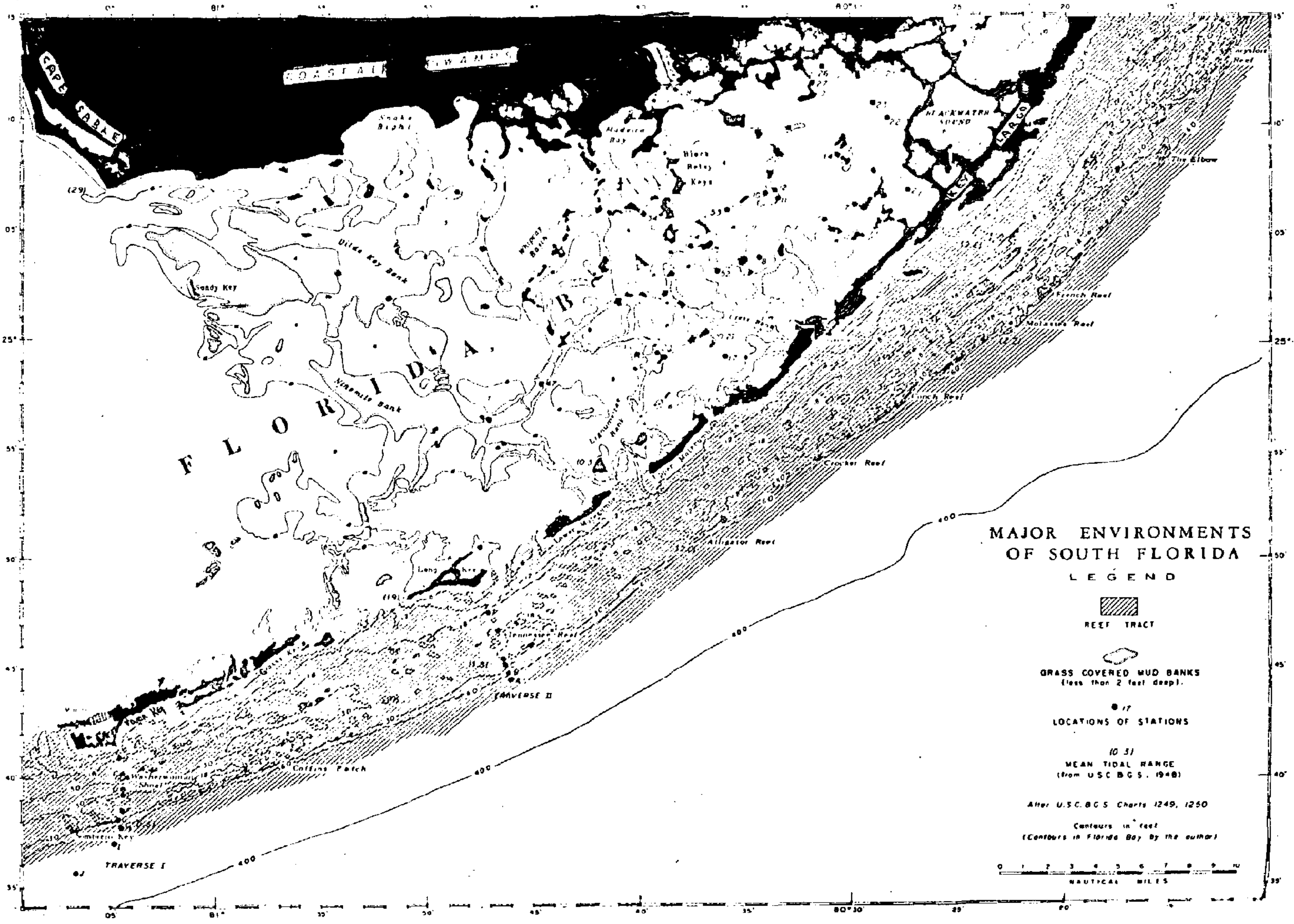
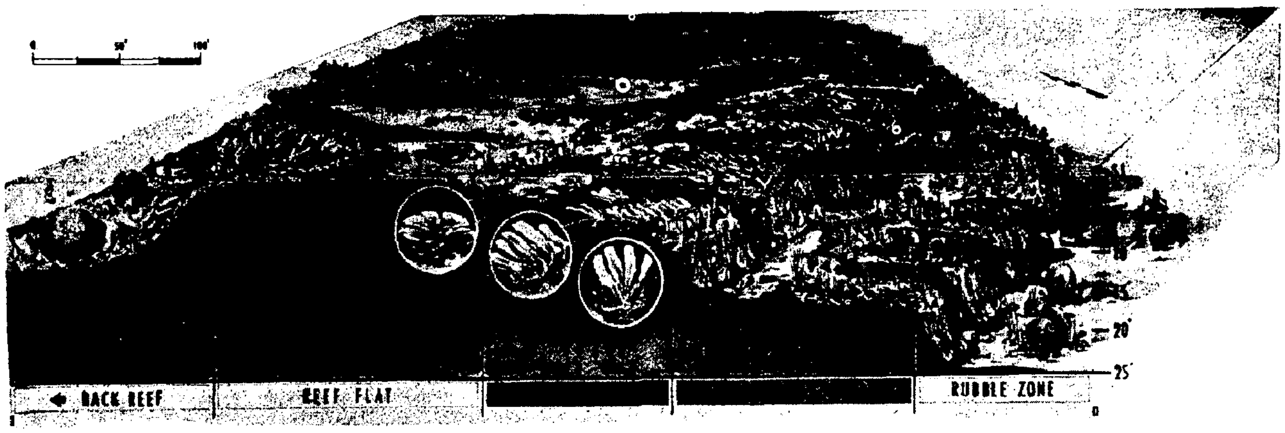
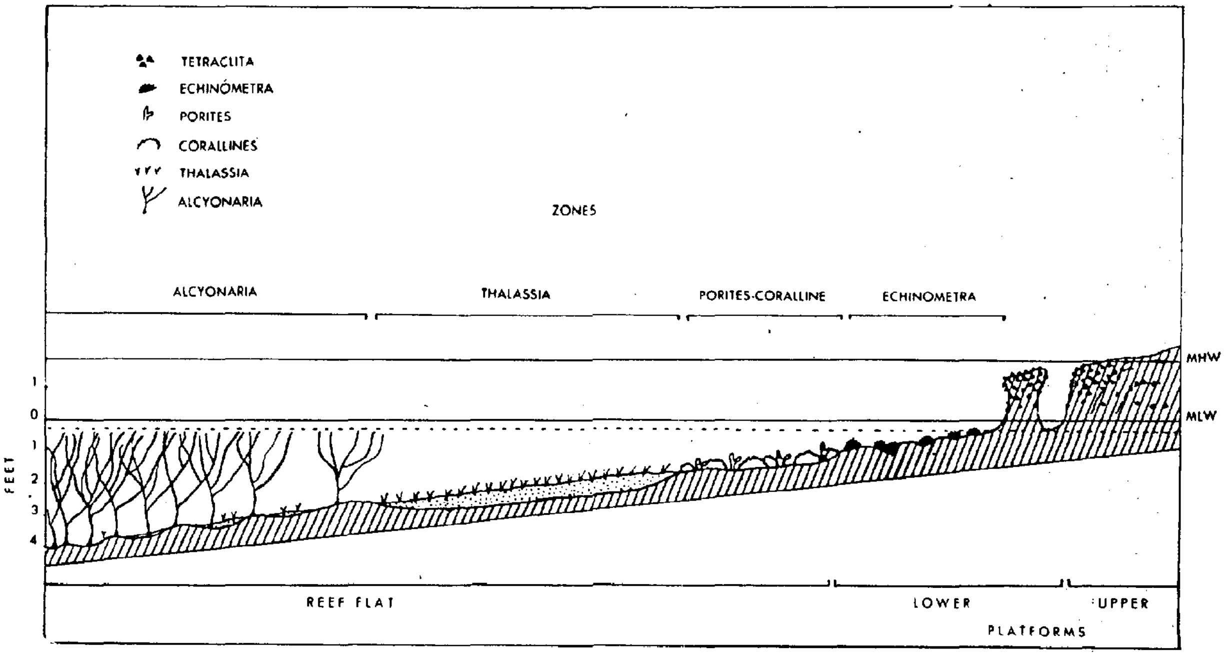

MAJOR ENVIRONMENTS OF SOUTH FLORIDA
LEGEND
▨ REEF TRACT
GRASS COVERED MUD BANKS (less than 2 feet deep).
● 17 LOCATIONS OF STATIONS
(0.3) MEAN TIDAL RANGE (from U.S.C.&G.S., 1948)
After U.S.C.&G.S. Charts 1249, 1250
Contours in feet
(Contours in Florida Bay by the author)
0 1 2 3 4 5 6 7 8 9 10
NAUTICAL MILES
FLORIDA BAY
COASTAL SWAMPS
CAPE SABLE
(2.9)
Snake Bight
Sandy Key
Nine Mile Bank
Whipray Basin
Black Betsy Keys
BLACKWATER SOUND
KEY LARGO
The Elbow
French Reef
Molasses Reef
Crocker Reef
Alligator Reef
Long Key
Tennessee Reef
Coffins Patch
TRAVERSE I
TRAVERSE II
400
81°
80°30'
25°

Fig. 22. Coastal features at the southern tip of Florida, showing reef distribution on the Florida tract. Reefs as in Fig. 24 occur at northern end of the tract, with structural complexity increasing southward. (Ginsburg et al.,1963).


0
50'
100'
BACK REEF
REEF FLAT
RUBBLE ZONE
20'
25'
0

Block diagram of Key Largo Dry Rocks showing ecologic zones and major types of *Acropora palmata* growth forms.

Fig. 23. Generalized diagram of reef morphology on Florida tract. Groove and spur system is in evidence, although not as well developed as on Jamaican or Pacific reefs. (Shinn, 1963).


TETRACLITA
ECHINOMETRA
PORITES
CORALLINES
THALASSIA
ALCYONARIA
ZONES
ALCYONARIA
THALASSIA
PORITES-CORALLINE
ECHINOMETRA
MHW
MLW
FEET
1
0
1
2
3
4
REEF FLAT
LOWER
UPPER
PLATFORMS

A diagrammatic transect seaward from the upper platform to a depth of 4 feet below mean low water (not drawn to scale). The slanting lines represent the solid rocky base, the stippled lines represent calcareous sands and mud. The horizontal broken line represents the level of mean low water springs. The horizontal distance shown is about 300 feet.

Fig. 24. A less well developed Florida reef occurring toward the northern limits for reef formation. (Voss and Voss, 1955.)

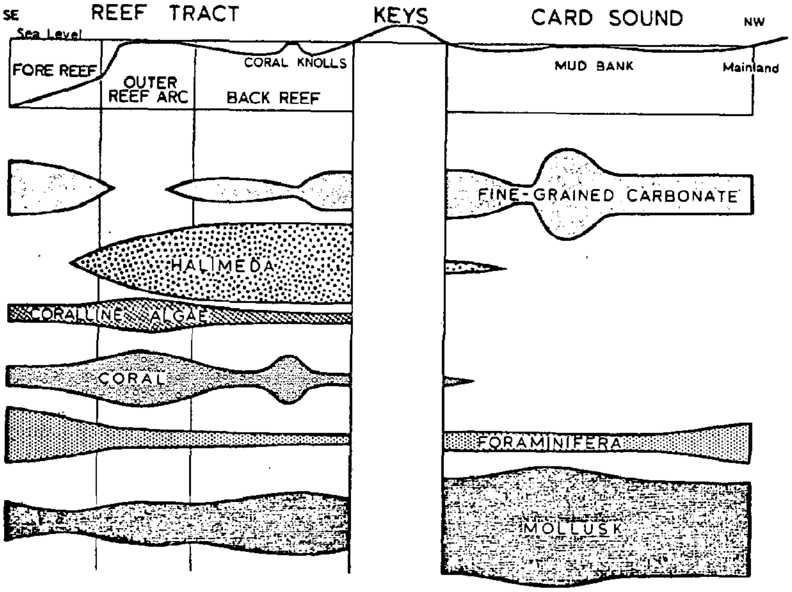

SE
REEF TRACT
KEYS
CARD SOUND
NW
Sea Level
FORE REEF
OUTER REEF ARC
CORAL KNOLLS
BACK REEF
MUD BANK
Mainland
FINE-GRAINED CARBONATE
HALIMEDA
CORALLINE ALGAE
CORAL
FORAMINIFERA
MOLLUSK

Figure 25. The upper portion of diagram shows cross section of the Florida reef tract. The distribution of sedimentary types is presented, showing the relative amounts of each type of calcareous sediment in the various environments. Fine grained carbonates may arise by chemical or bacterial precipitation from seawater. Halimeda is a common green alga with a free standing thallus made of calcified blade-shaped "leaves"; at death, the "leaves" crumble to form a fine calcareous sediment. Foraminifera are individual microscopic organisms (Protozoa) which produce tiny calcareous skeletons, each of which becomes a "sand grain" upon death of the animal. (Earley 1967, modified after Ginsburg, 1956).

Table 2. Productivity measurements on individual corals by oxygen measurement. The corals show ability to produce 1.9 to 5.8 times more oxygen than they consume. (Kanwisher and Wainwright, 1967).

Calculated values of gross photosynthesis per unit surface area, maximum observed ratios of photosynthesis/respiration, and observed or estimated photosynthetic compensation light intensities for some Florida reef corals

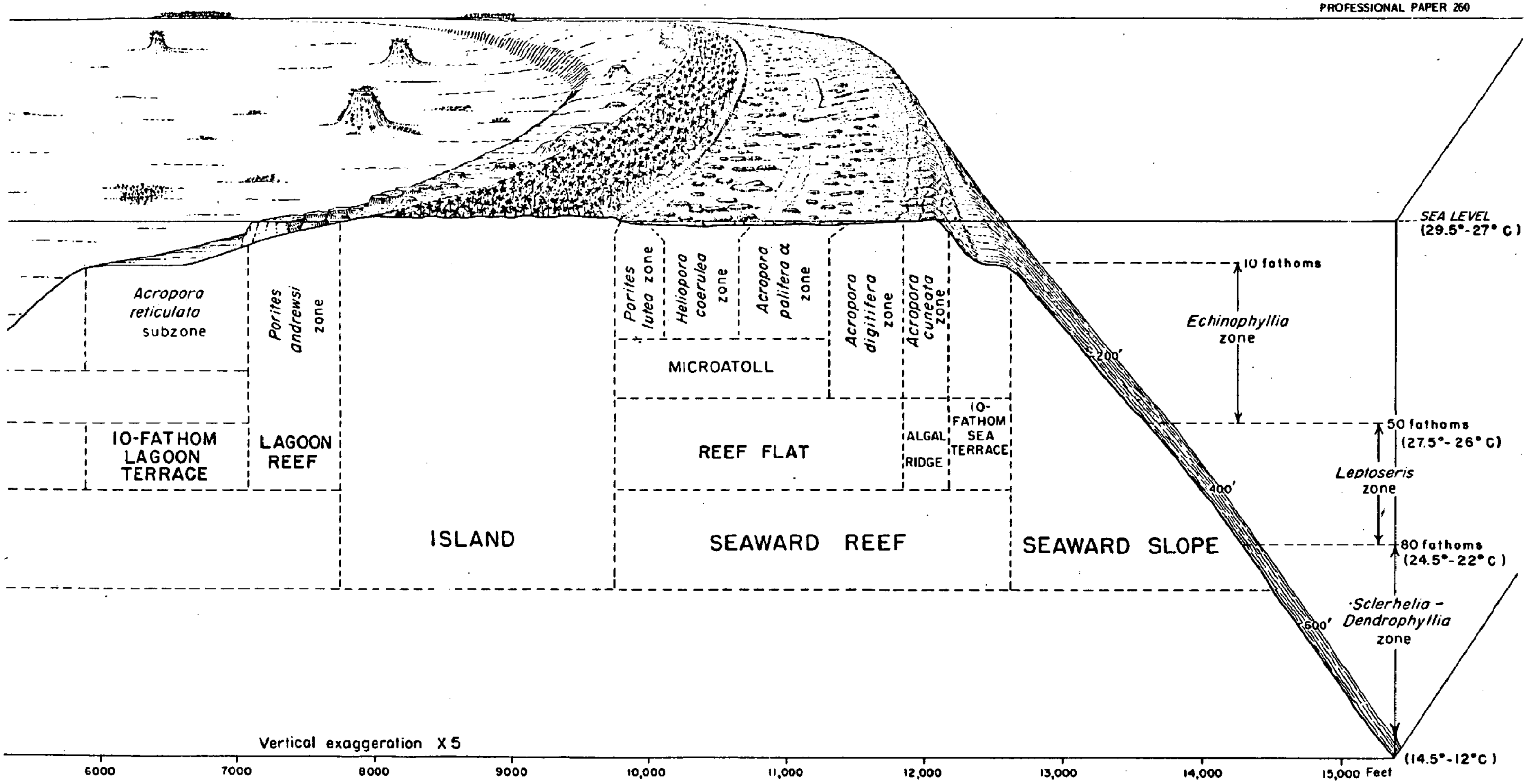
Species	Gross photosynthesis q. C/m^2./day	Maximum photosynthesis / respiration	Compensation light intensity in footcandles
Gorgonacea			
Plexaura flexuosa	6.5	5.8	400
Gorgonia ventalina	6.8	3.0	300
Briareum asbestinum	3.7	2.5	400
Erythropodium caribaeorum	5.8	4.2	600
Scleractinia			
Siderastrea siderea	4.0	2.1	300
Porites divaricata	10.2	3.4	600
Favia fragum	4.2	2.3	400
Manicina areolata	5.2	2.4	—
Montastrea annularis	9.5	2.9	200
Oculina diffusa	8.4	5.0	—
Dichocoenia stokesii	8.0	—	300
Mussa angulosa	2.7	1.9	300
Isophyllia multiflora	7.9	5.0	400
Colpophyllia sp.	5.4	3.2	700

Table 3. Productivity measurements performed in the vicinity of reefs at the northern end of the Florida tract. (Jones 1963).

PRODUCTIVITY VALUES OBTAINED FROM LIGHT-DARK BOTTLE EXPERIMENTS AND NET OXYGEN GAIN IN WATER BETWEEN 0600 AND 1200 DAILY

	1961		1962	
	Aug.	Nov.	Mar.	May
Gross, Bottle Experiments:				
Oxygen Gain (ml/L/day)	0.06	0.78	0.04	0.06
Carbon Fixed				
(mg/L/day)	0.03	0.42	0.02	0.03
(g/m^2/day)	0.06	0.84	0.04	0.06
Net, Bottle Experiments.				
Oxygen Gain (ml/L/day)	0.02	0.52	0.04	0.00
Carbon Fixed				
(mg/L/day)	0.01	0.28	0.02	0.00
(g/m^2/day)	0.02	0.56	0.04	0.00
Net Change in Ambient Water:				
Oxygen Gain (ml/L/day)	1.84	0.88	0.78	1.66
Carbon Fixed				
(mg/L/day)	0.99	0.47	0.42	0.89
(g/m^2/day)	1.97	0.94	0.84	1.78

PROFESSIONAL PAPER 260


SEA LEVEL
(29.5°-27° C)
10 fathoms
Echinophyllia zone
50 fathoms
(27.5°-26° C)
Leptoseris zone
80 fathoms
(24.5°-22° C)
·Sclerhelia - Dendrophyllia zone
(14.5°-12°C)
200'
400'
600'
Acropora reticulata subzone
Porites andrewsi zone
Porites lutea zone
Heliopora coerulea zone
Acropora palifera α zone
Acropora digitifera zone
Acropora cuneata zone
MICROATOLL
10-FATHOM LAGOON TERRACE
LAGOON REEF
REEF FLAT
ALGAL RIDGE
10-FATHOM SEA TERRACE
ISLAND
SEAWARD REEF
SEAWARD SLOPE
Vertical exaggeration X 5
6000
7000
8000
9000
10,000
11,000
12,000
13,000
14,000
15,000 Feet

ZONAL ANALYSIS OF CORAL FAUNA AT BIKINI ATOLL

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Fig. 26. Cross sectional view of the windward edge of Bikini Atoll, Marshall Islands. Coral Knolls can be seen in the lagoon region. (Wells, 1954).

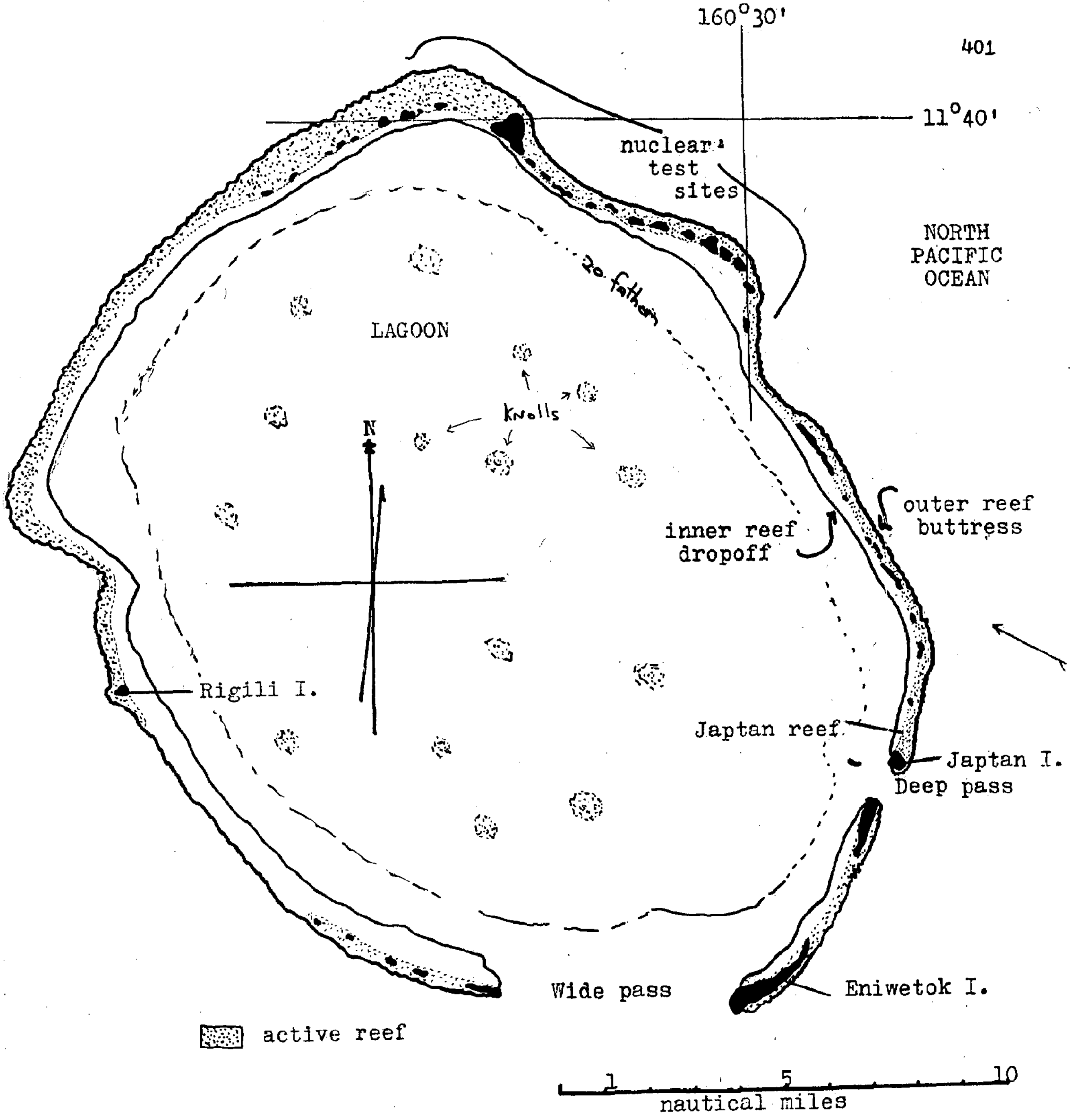

160°30'
11°40'
nuclear test sites
NORTH PACIFIC OCEAN
LAGOON
20 fathom
knolls
N
inner reef dropoff
outer reef buttress
Rigili I.
Japtan reef
Japtan I.
Deep pass
Wide pass
Eniwetok I.
▨ active reef
1
5
10
nautical miles

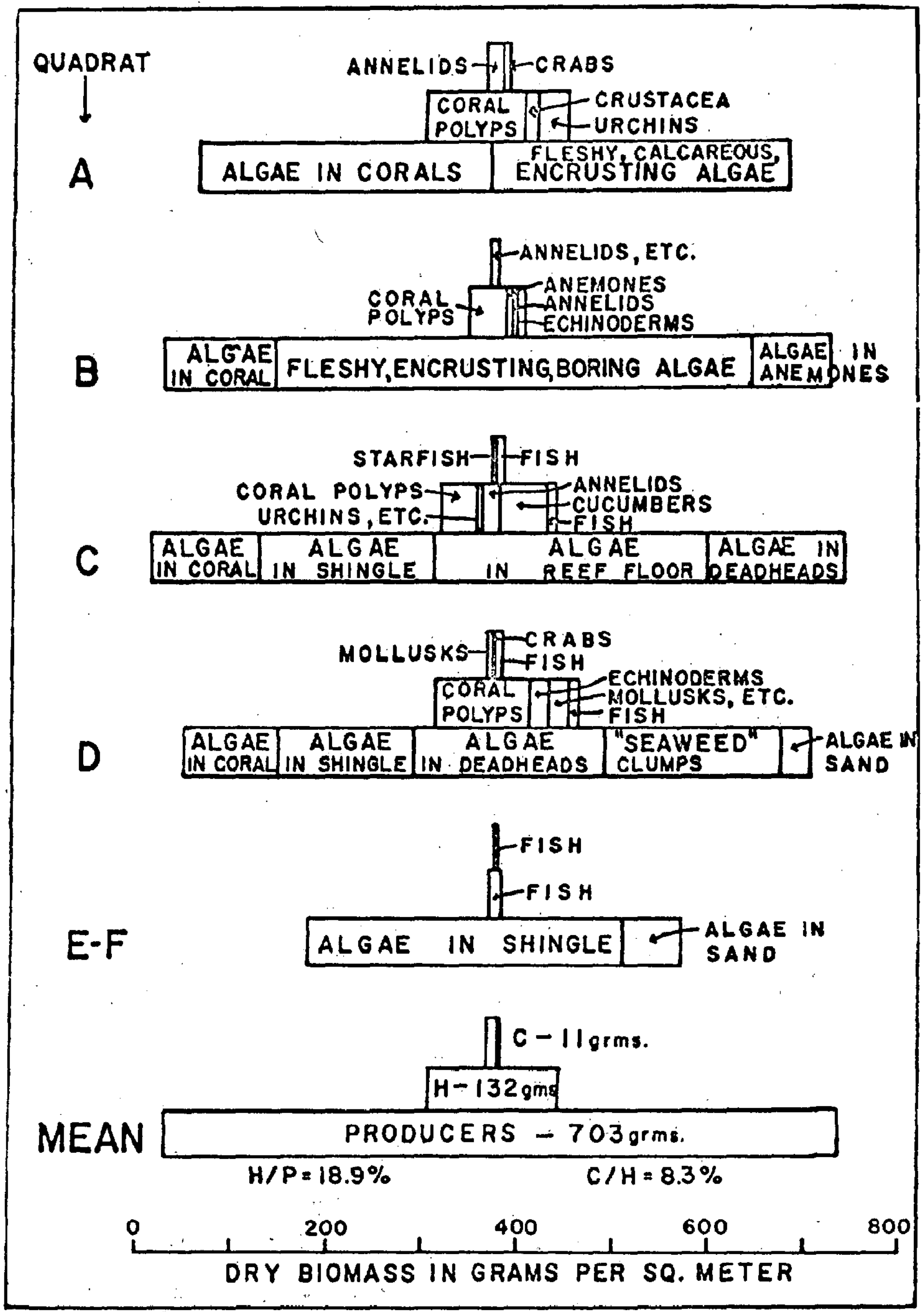
Fig. 27. Eniwetok Atoll, Marshall Islands. This is a circular atoll with about 40 islets, lagoon of max, depth 200 ft., and two major passes through the reef. Knoll reefs dot the lagoon. Islets are in black, and reef areas stippled are awash at low tide. (DiSalvo modification of Hines, 1962).

Estimates of biomass of animals on quadrats are given by Odum and Odum (1955) for Japtan reef, Eniwetok (Fig. 28). The unidirectional flow of water over the reef allowed determination of changes in community structure and water quality at successive stations across the reef from upstream to downstream (Figs. 29 and 30 and Tables 4 and 5). Estimates of metabolism from oxygen curves in Fig. 29 are given by Helfrich and Townsley(1965) in Table 6. Reef nutrition through removal of dissolved materials from seawater was hypothesized by Doty (1958), and laboratory evidence favors this assumption. Examples illustrated are the work of Yonge (1931) who showed that Australian corals could remove phosphorus from seawater (Fig. 8) and Kawaguti (1953) who showed that corals removed ammonium compounds (Fig. 7).

In unpublished tracer experiments DiSalvo found that hermatypic corals could remove certain divalent cations from sea water. Stevens (1962) similarly found corals removing dissolved organic substances. The reef may be withdrawing and recapturing substances from its overlying waters as indicated in Fig. 29 for Eniwetok. Some particulate matter is exported to the lagoon (Fig. 29, Table 4, and Marshall, 1968 and Johannes 1967). Highly relevant are studies tracing pathways taken by radionuclides released into oceanic waters during nuclear testing. Many reports (See bibliography in Hines 1962) have demonstrated high radioactivity uptake in reef corals collected at Eniwetok and Bikini including rare earth elements. Effects of these nuclides on the coral tissues are not known, although atypical growths resembling calcareous tumors have been described for a few corals recovered from bomb test areas (Hines, 1962). Rapid decay of radioactive and specific differences are indicated by data such as those in Fig. 31. The reefs are highly specialized for retention and recycling of materials, and studies on detrital release by reefs at Eniwetok and elsewhere have not shown as yet that significant quantities or organic matter are released from the reef (Johannes, 1967; Marshall, 1968).

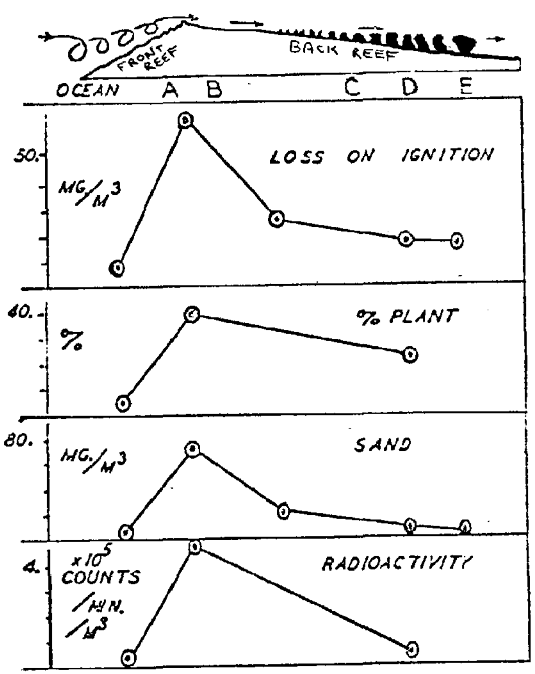
Hiatt and Strasburg (1960) present the food web of a coral reef in Fig. 32. They show feeding relationships of reef fishes (Figs. 33-35) which control passage of fission products through complex reef food chains, (Fig. 31). So little was known about the functional biology of the coral reef ecosystem prior to nuclear weapons testing that the after-effects of this disturbance remain obscure. Reef areas near test sites are undergoing recolonization by corals and other invertebrates, although large areas are covered by atypically occurring filamentous algae (personal observation, Di Salvo, 1964). Physical damage done by the bombs approximated the damage that might be expected from a typhoon (Wiens, 1962) except in the immediate vicinity of the blast where reefs were destroyed by direct shock and radiation. Residual turbidity affects recovery.

A milder type of reef disturbance has been observed by Brock et al. (1966) at Johnston Atoll, to the east of the Marshall Islands. At this military base the creation of new land from reef areas by dredging (Fig. 54) has resulted in the siltation of widespread reef areas with concomitant change in the environment. A new system may be developing as evidenced by changed structure, diminished diversity of animals, and increased population of the substrate by atypical species of filamentous algae. Some of these changes are outlined in Tables 12 and 13.



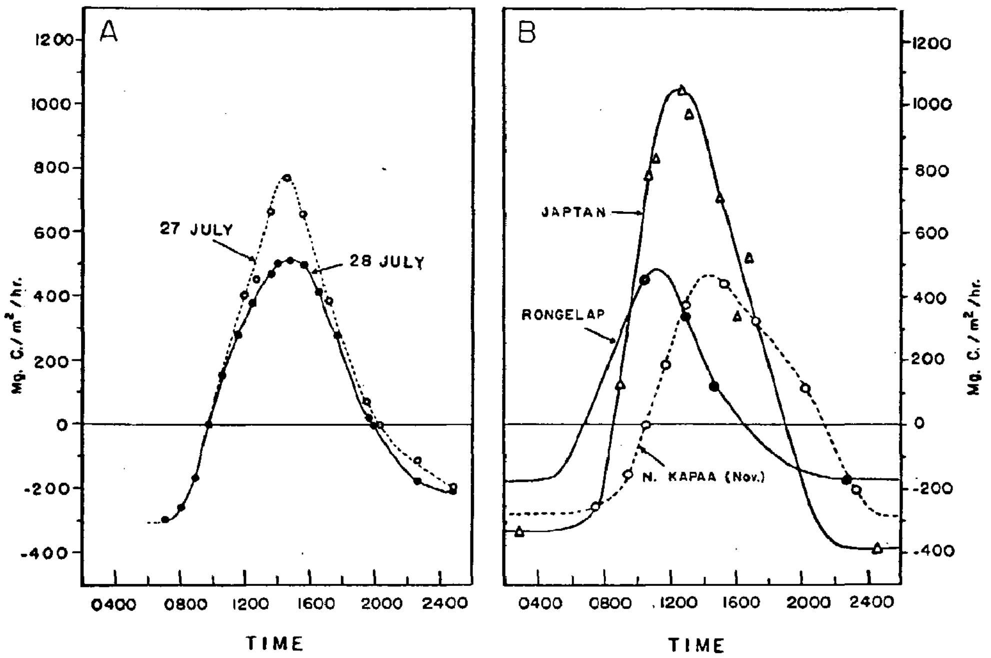
Pyramids of biomass resulting from estimates of the dry weight of living materials (excluding, of course, dead skeletal materials associated with protoplasm). For each quadrat, A-F, the weight of "producers" (bottom layer of pyramid), the "herbivores" (H) (middle layer), and the "carnivores" (C) (top layer) is shown, and also the average dry biomass for the reef.

Fig. 28. Estimates of biomass in six distinct zones found across the Japtan reef, (Fig. 27), Eniwetok Atoll. Zone "A" was located on the reef flat behind the buttress zone, "B", "C", "D" were zones of successively larger coral heads across the reef, and zones "E-F" were lagoonward sandy back reef areas. (Odum and Odum, 1955).



Changes in water content as it crosses the reef in regard to: loss on ignition of net plankton and seston; green plant content (estimated by chlorophyll content) of net plankton; suspended sand; radioactivity.

Fig. 29. Changes in water over Japtan reef, Eniwetok. (Odum and Odum, 1955).



Production and consumption of organic matter. *A*, North Kapaa Reef, 27 July 1956 and 28 July 1956. *B*, North Kapaa Reef, 25 November 1955; reef at Japtan Island, Eniwetok Atoll; and reef at Bokujarito Island, Rongelap Atoll. Data not corrected for diffusion. Data from Japtan and Bokujarito are from Odum and Odum (1955) and Sargent and Austin (1954), respectively.

Fig. 30. Diurnal curves obtained in coral reef studies, showing that total organic production only slightly exceeds consumption on the reefs studied. Results are derived from oxygen measurements made on reef waters. (Kohn and Helfrich, 1957).

Table 4. Organic inputs and outputs over the Japtan reef. (Odum and Odum, 1955).

Balance sheet for the Japtan inter-island reef in July. From algal-coral ridge to the end of the zone of large heads, this zone is 322 m^2 long.

	$gm/m^2/day$
INCOME*	
Planktonic organic matter (Table 13) from breaker zone	2.0‡
Primary production (measured as oxygen, calculated as glucose:	
Net (uncorrected) daytime production	14.0
Respiration during daytime	10.0
Total income	26.0
LOSSES*	
Planktonic organic matter lost to lagoon (Table 13)	0.4‡
Total respiration in 24 hr	24.0
Total outgo	24.4

*Dissolved Organic Matter; 0.96 gm/m^3 (Table 14) (no significant difference between influx and outflux; analytical method not precise enough, however, to delimit.)

‡The mean water flux during plankton sampling was $425m^3/hr$ across a band of reef 1 m wide.

Table 5. Chemical levels in Eniwetok waters. (Odum and Odum, 1955).

Component	Analyses	Mean	Range
Organic Matter, alkaline permanganate method, in mg/l	13	.96	.74—1.41
Nitrate nitrogen, strychnidine method, in mg atoms/m^3	24	.44	.06—1.0
Inorganic phosphorus, ammonium molybdate method in mg atoms/m^3	29	.32	.26—.64
Total phosphorus, acid digested, in mg atoms/m^3	6	1.7	0—3.4
Dissolved oxygen, Winkler method, in mg/l.			
(1) Incoming Ocean Water (from channel)	8	6.54	6.38—6.65
(2) Algal-coral Ridge	12	6.50	6.09—6.97
(3) Back Reef zone of Large Heads			
Daytime	19	7.31	6.22—8.50
Night	6	5.37	4.89—6.29
pH (Beckman Model G)			
Daytime			
Incoming Ocean Water (from channel)	5	8.21	8.19—8.22
Algal-coral ridge	5	8.21	8.19—8.24
Back Reef zone of large heads	5	8.32	8.30—8.33
Night			
Incoming Ocean Water (from channel)	2	8.19	8.18—8.19
Algal-coral ridge	2	8.16	8.14—8.17
Back Reef Zone of large heads	2	8.10	8.10—8.10
Temperature in degrees Fahrenheit			
Incoming ocean water (from channel)	2	82.6	82.6—82.7
Algal-coral ridge	2	82.9	82.7—83.0
Back reef zone of large heads			
Daytime	3	84.1	83.5—84.6
Nighttime	1	82.2	....

Table 6. Summarized results of coral reef productivity measurements compared to similar measurements performed in other marine environments. (Helfrich and Townsley, 1965).

LOCATION	GROSS PRODUCTIVITY GRAMS CARBON/ m^2/YEAR	REFERENCE
Coral Reefs		
El Mario Reef, Puerto Rico	7,117[a]	Odum, Burkholder, and Rivero (1959)
Eniwetok Atoll, Marshall Islands	4,200[b]	Odum and Odum (1955)
N. Kapaa Reef, Kauai, Hawaii	2,900	Kohn and Helfrich (1957)
Rongelap Atoll, Marshall Islands	1,800[b]	Sargent and Austin (1954)
Turtle Grass Beds		
Long Key, Florida	4,650	Odum (1956)
Redfish Bay, Port Aransas, Texas	2,080	Odum and Hoskin (1958)
Open Ocean		
Benguela Current	167-912	Steemann Nielsen (1954)
Sargasso Sea	167	Riley, Stommel, and Bumpus (1949)
Off Hawaii	37	Steemann Nielsen (1954)
Off Rongelap Atoll, Marshall Islands	28	Sargent and Austin (1954)
Off Hawaii	21[c]	Doty and Oguri (1956)

[a] Average of 11 determinations.
[b] Standard diffusion correction applied to published data.
[c] Average of determinations from stations 1 and 2.

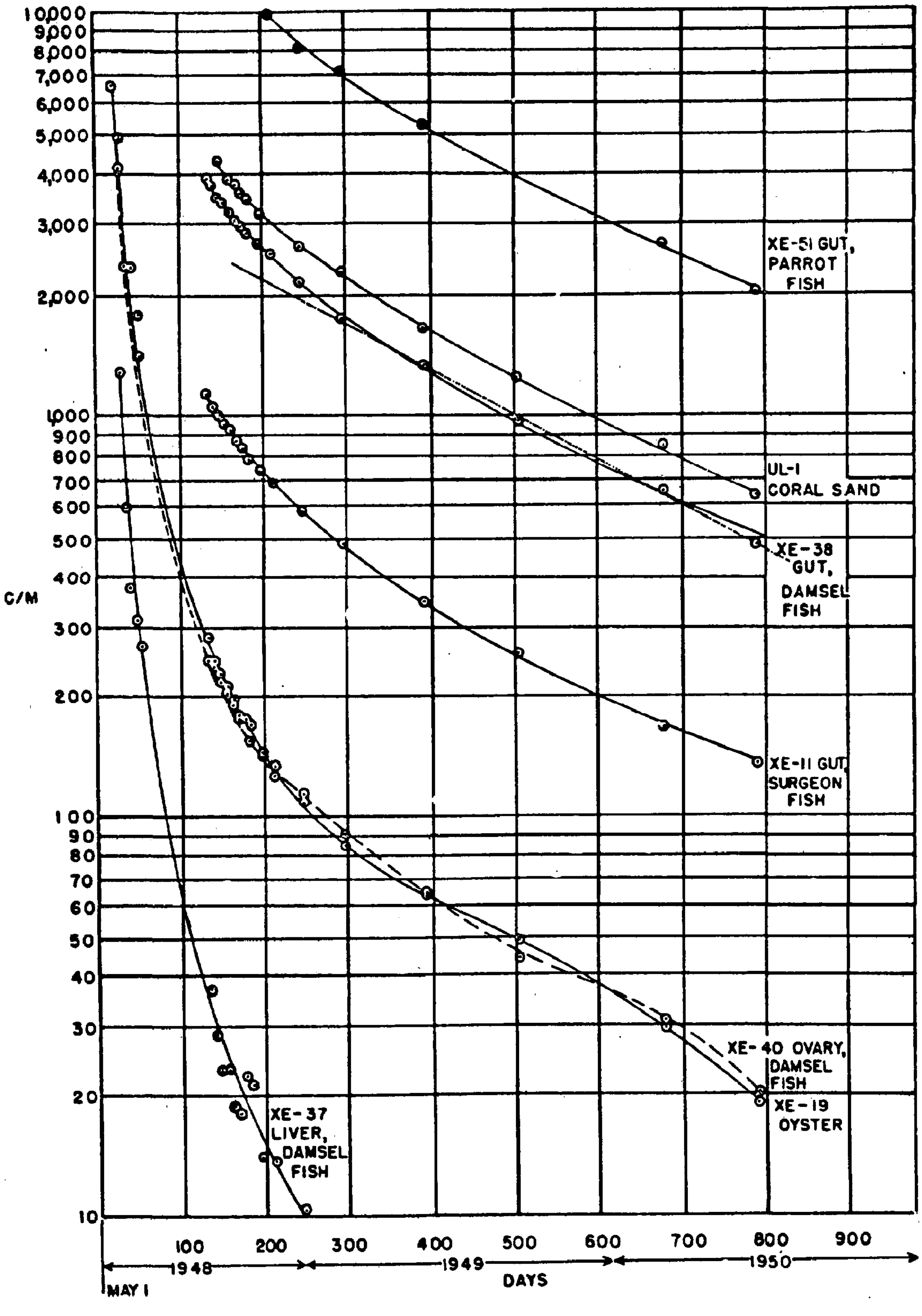


Fig. 31. Decline in radioactivity of fishes and sand collected over a two year period after nuclear weapons testing at Eniwetok Atoll. (Donaldson ,1960).

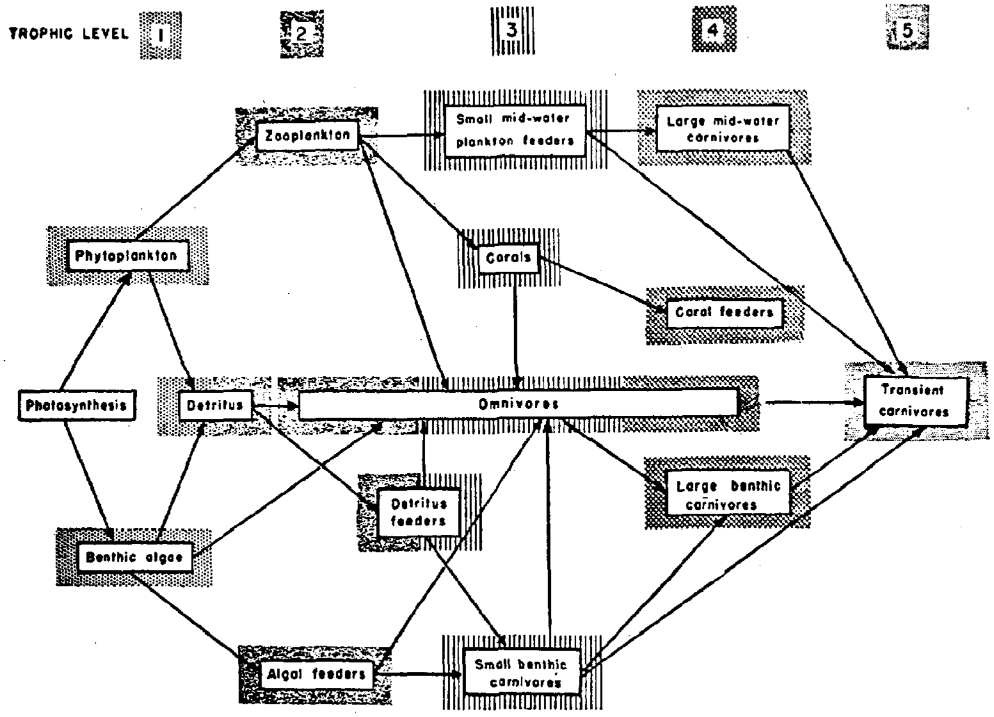

TROPHIC LEVEL
1
2
3
4
5
Zooplankton
Small mid-water plankton feeders
Large mid-water carnivores
Phytoplankton
Corals
Coral feeders
Photosynthesis
Detritus
Omnivores
Transient carnivores
Detritus feeders
Large benthic carnivores
Benthic algae
Algal feeders
Small benthic carnivores

Fig. 32. A hypothetical food web to describe the complex trophic(feeding) relationships on a coral reef. Constructed from data obtained in a comprehensive study of Marshall Island fishes. Trophic levels 1-5 represent primary producers, herbivores, and three levels of carnivore, respectively. (Hiatt and Strasburg, 1960).

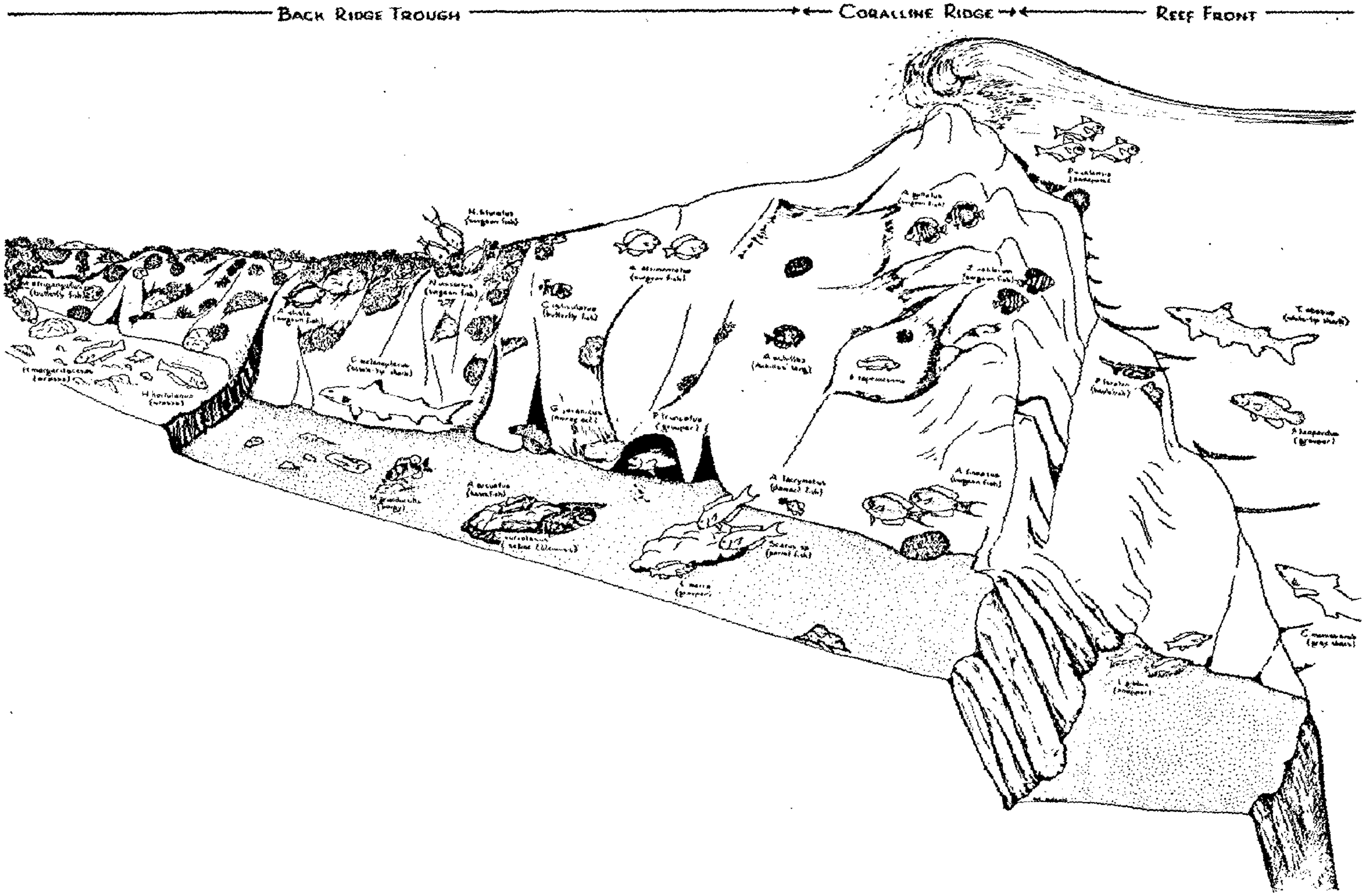

BACK RIDGE TROUGH
CORALLINE RIDGE
REEF FRONT
(butterfly fish)
A. olivaceus (surgeon fish)
(wrasse)
H. hortulanus (wrasse)
C. melanopterus (black-tip shark)
(surgeon fish)
(surgeon fish)
(butterfly fish)
(surgeon fish)
G. javanicus (moray eel)
P. truncatus (grouper)
A. achilles (Achilles' tang)
A. guttatus (surgeon fish)
Z. veliferum (surgeon fish)
A. lacrymatus (damsel fish)
A. lineatus (surgeon fish)
A. arcuatus (hawkfish)
M. grandoculis (porgy)
Scarus sp. (parrot fish)
C. merra (grouper)
T. obesus (white-tip shark)
A. leopardus (grouper)
C. menisorrah (gray shark)

Fig. 33. A conceptual diagram of reef structure and fish fauna of the surge channel and surf zone of a Marshall Island reef. Fishes are shown in characteristic feeding attitudes. (Hiatt and Strasburg, 1960).

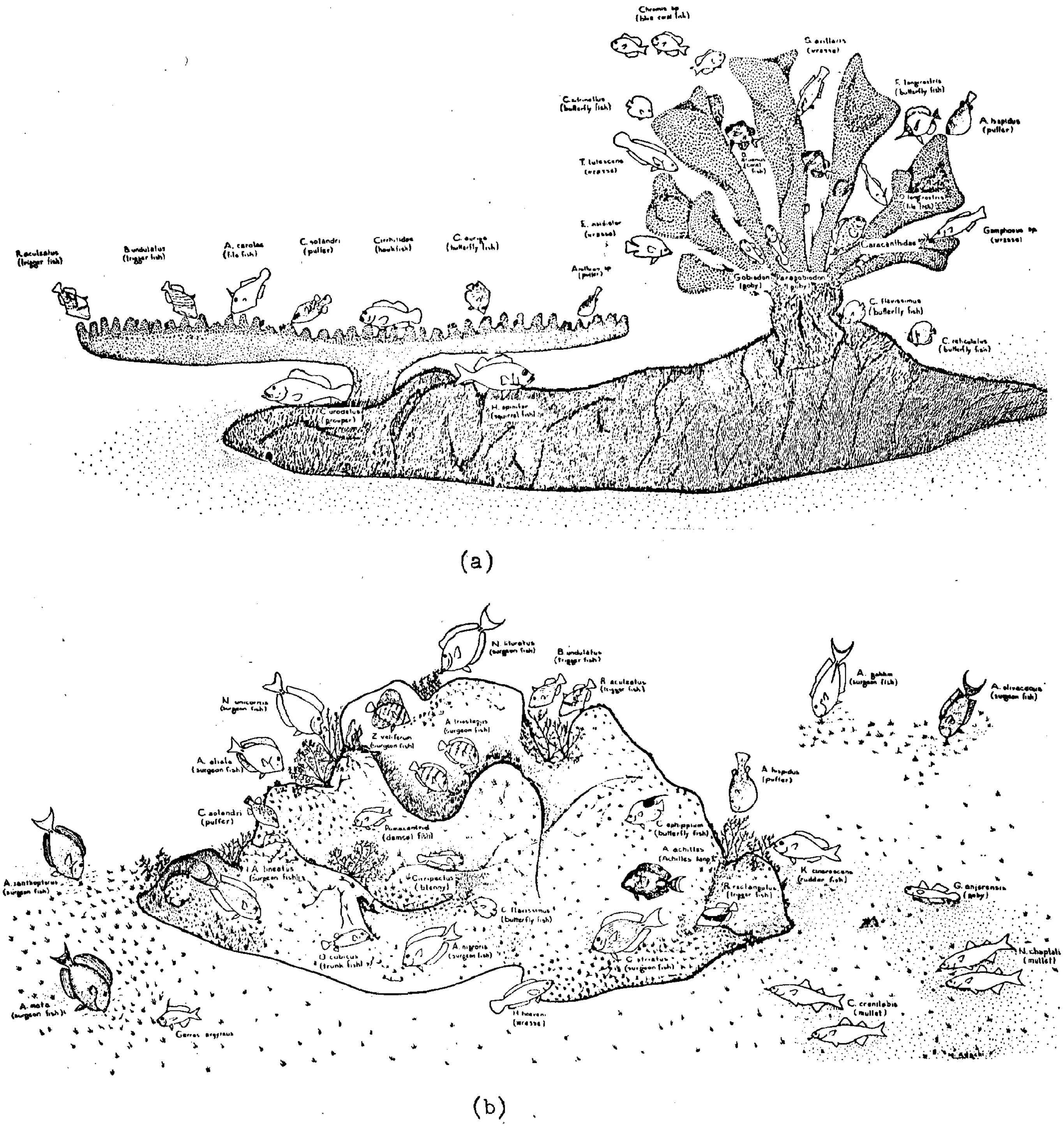

Chromis sp. (blue coral fish)
S. axillaris (wrasse)
F. longirostris (butterfly fish)
C. trifasciatus (butterfly fish)
A. hispidus (puffer)
T. lutescens (wrasse)
D. aruanus (coral fish)
O. longirostris (file fish)
E. insidiator (wrasse)
Gomphosus sp. (wrasse)
Caracanthidae
R. aculeatus (trigger fish)
B. undulatus (trigger fish)
A. carolae (file fish)
C. solandri (puffer)
Cirrhitidae (hawkfish)
C. auriga (butterfly fish)
Anthias sp. (puffer)
Gobiodon (goby)
Paragobiodon (goby)
C. flavissimus (butterfly fish)
C. reticulatus (butterfly fish)
C. urodelus (grouper)
H. spinifer (squirrel fish)
(a)
N. lituratus (surgeon fish)
B. undulatus (trigger fish)
R. aculeatus (trigger fish)
A. guttatus (surgeon fish)
A. olivaceous (surgeon fish)
N. unicornis (surgeon fish)
A. triostegus (surgeon fish)
Z. veliferum (surgeon fish)
A. elliptus (surgeon fish)
A. hispidus (puffer)
C. solandri (puffer)
Pomacentrid (damsel fish)
C. ephippium (butterfly fish)
A. achilles (Achilles tang)
A. xanthopterus (surgeon fish)
A. lineatus (surgeon fish)
Cirripectus (blenny)
R. rectangulus (trigger fish)
K. cinerascens (rudder fish)
G. anjerensis (goby)
C. flavissimus (butterfly fish)
O. cubicus (trunk fish)
A. nigroris (surgeon fish)
C. striatus (surgeon fish)
N. chaptali (mullet)
A. mata (surgeon fish)
Gerres argyreus
H. hoeveni (wrasse)
C. crenilabis (mullet)
Adachi
(b)

Fig. 34. (a) Fishes associated with branching corals as noted for Marshall Island reefs.
(b) Herbivorous fish in characteristic feeding attudes as seen on Marshall Island reefs. (Hiatt and Strasburg, 1960).

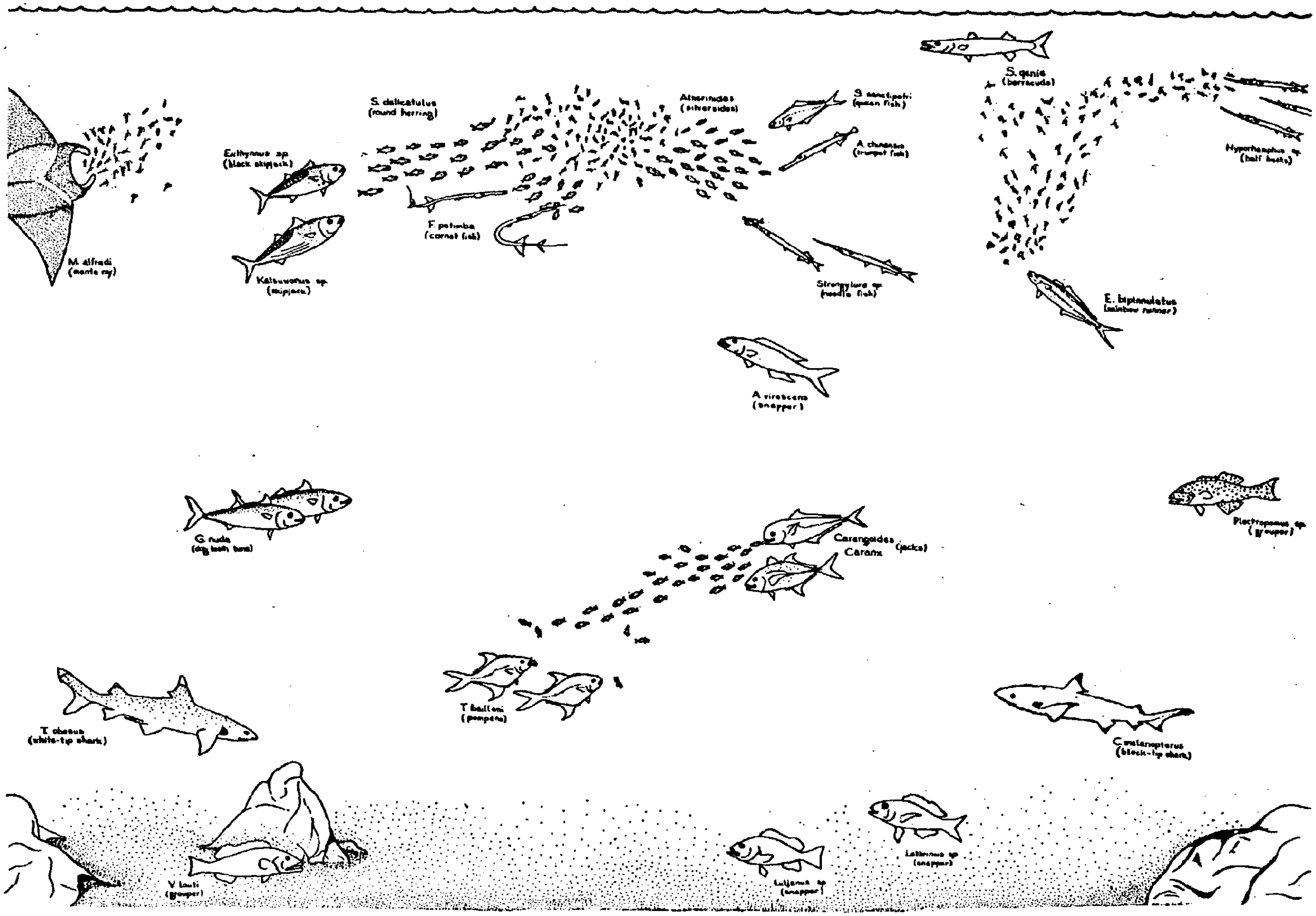

M. alfredi
(manta ray)
Euthynnus sp.
(black skipjack)
Katsuwonus sp.
(skipjack)
S. delicatulus
(round herring)
F. petimba
(cornet fish)
Atherinidae
(silversides)
S. sanctipetri
(queen fish)
A. chinensis
(trumpet fish)
Strongylura sp.
(needle fish)
S. genie
(barracuda)
Hyporhamphus sp.
(half beaks)
E. bipinnulatus
(rainbow runner)
A. virescens
(snapper)
G. nuda
(dog tooth tuna)
Carangoides
Caranx
(jacks)
Plectropomus sp.
(grouper)
T. obesus
(white-tip shark)
T. bailloni
(pompano)
C. melanopterus
(black-tip shark)
V. louti
(grouper)
Lutjanus sp.
(snapper)
Lethrinus sp.
(snapper)

Fig. 35. The mid-water surface community as found near coral reefs of the Marshall Islands. (Hiatt and Strasburg, 1960).

Whereas the aforementioned studies of ocean-lagoon water flow across Japtan reef (Odum and Odum, 1955) concerned an inter-island reef at Eniwetok, there are similarities between it and the fringing reef of Bikini Atoll where water washed onto the reef returns to the ocean by percolating down through tunnels in the buttress"honeycomb"area (Figs. 26, 36).

Hawaiian Coral Reefs; Kaneohe Bay, Oahu

The Hawaiian Islands (Fig. 37) are a showcase demonstrating geological emergence and subsidence with concomitant formation of coral reefs. Fringing reefs (Figs. 38 and 39) are found around the coasts of the younger islands, where incipient reef formation has been studied (Doty,1967c; Oostdam 1963). The northernmost islands of the Hawaiian chain are the atolls of Midway and Kure. Rock corings at Midway (Fig. 10; Ladd et al; 1967) showed the presence of reef limestone and shallow water fossils to a depth of over 1000 ft. capping parent volcanic basalt. This deposition was estimated to have taken over 30 million years.

Fig. 29 and Table 6 from Helfrich and Townsley(1965) show the reefs in Hawaii to be in the same productivity class as the Pacific atoll reefs. The steady pattern of life histories and larval release was established by Edmondson and Ingram (1939) (Fig. 40). Although the temperature shift is only a few degrees between seasons, a pulse in reproductive activity was registered, with apparent favoring of the summer season of greater light for productivity. Brock (1954) has provided relative species and biomass estimates for fishes of several Hawaiian reefs (Fig. 41). Some quantitative biomass estimates for leeward Oahu reefs (Fujimura, 1960) are presented in Fig. 42. Distribution patterns and niche substitution in carnivorous cones were studied by Kohn (Fig. 43). A wealth of taxonomic and descriptive information has been published about the fauna of Hawaiian reefs, including reviews of fishes (Gosline and Brock, 1960), sponges (De Laubenfels, 1950), didemnid ascidians (Eldredge, 1965), snapping shrimp (Banner, 1953) molluscs (Tinker, 1958) and others (see Edmondson, 1946b).

Kaneohe Bay, Oahu (Figs. 37 and 44) is the site of the University of Hawaii Marine Laboratory and is also the site of intensive study on the influence of stress on an environmentally diverse tropical bay. The extensive development of reefs in Kaneohe Bay is attributed to the presence of a Hawaiian barrier reef (Moberly and Chamberlain 1964; Fig. 45). This reef extends almost the entire length of the bay, providing a natural breakwater while allowing a constant overflow of clean waters in a wind and tide-driven circulation (Fig. 46) similar to that described for atolls Von Arx, 1954 ; Bathen 1968). This bay has been receiving heavy flows of sewage at its southern end, causing high phosphate values as depicted in Fig. 47. Freshwater inflows in addition to sewage inputs produce salinity changes and increases in turbidity as illustrated in Figs. 48, 49 and Tables 7, 8. The changing pattern of the system includes development of plankton-base characteristics (Peterson, MS Thesis, Dept. of Oceanography, University of Hawaii, 1968) effects on shoreside clam beds (Higgins,MS Thesis, Dept. of Oceanography, University of Hawaii, 1968) and development of bluegreen algae-worm-oyster reefs (DiSalvo, personal observations). The development of the oyster, Ostrea gigas on seawalls at Coconut Island in Kaneohe Bay was noted by A. J. Kohn. to have occurred since 1954 (personal communication). Some of these effects are undoubtedly related to the coral reef freshwater kill of 1965 (Figs. 50

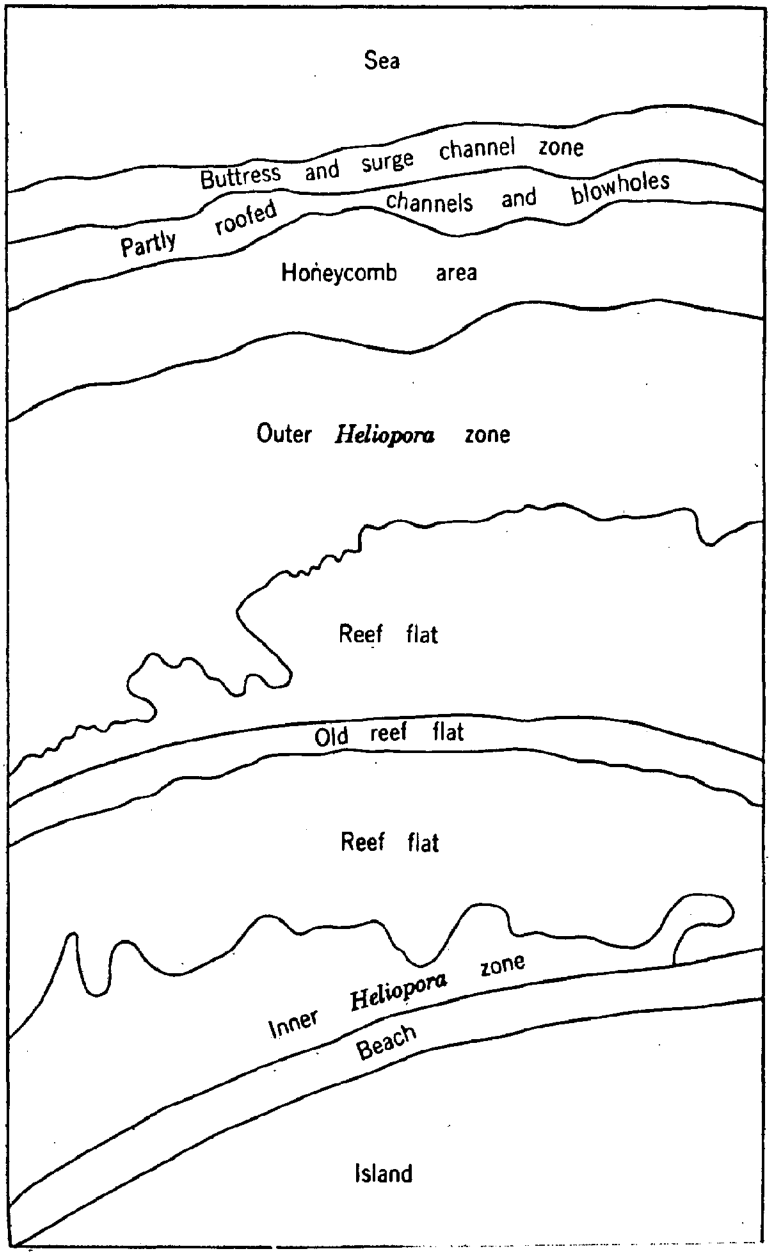
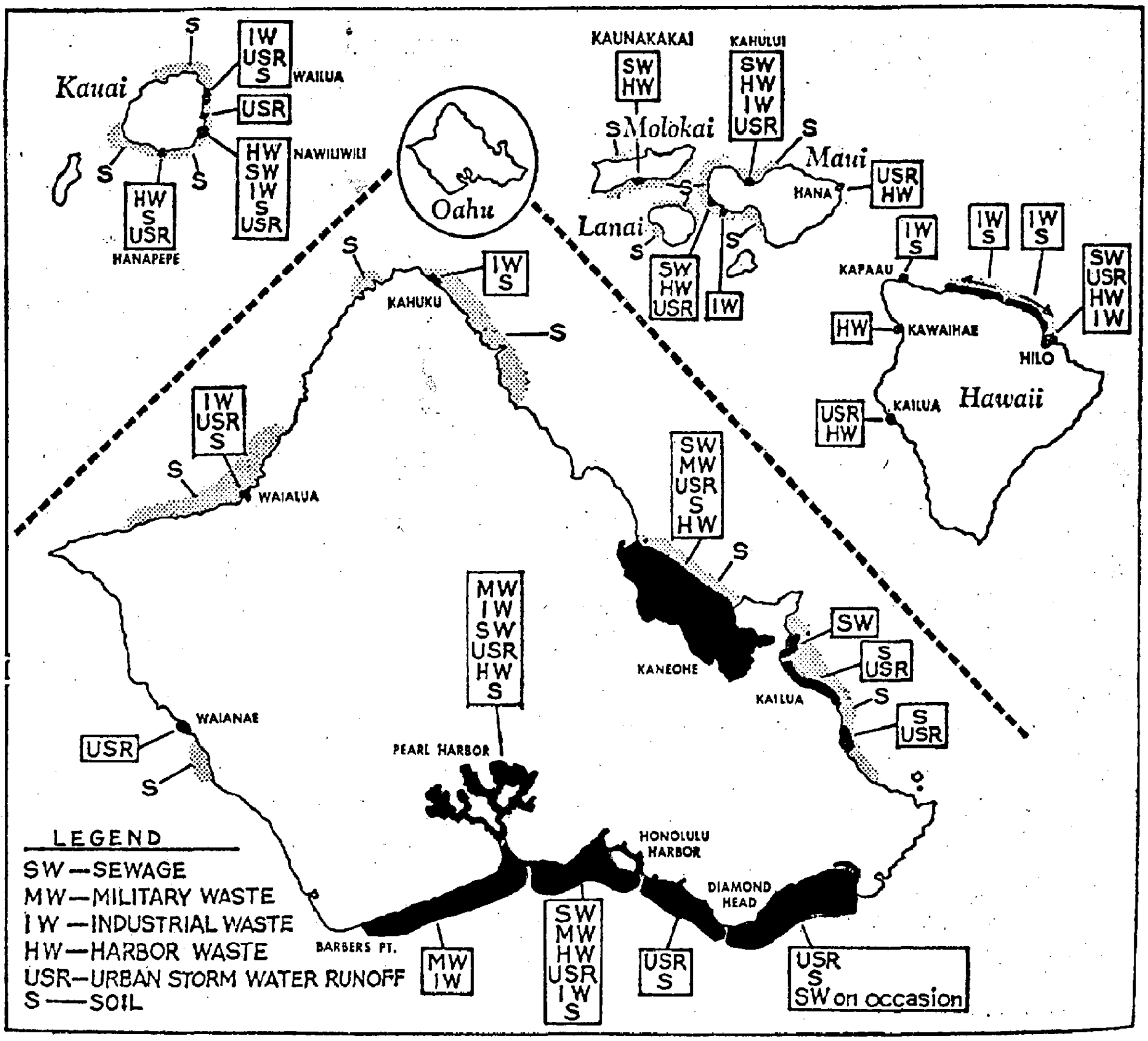

Sea
Buttress and surge channel zone
Partly roofed channels and blowholes
Honeycomb area
Outer *Heliopora* zone
Reef flat
Old reef flat
Reef flat
Inner *Heliopora* zone
Beach
Island

Fig. 36. Oceanic reef zonation at Bikini Atoll. See also figures 16 and 26. (Emery, Tracey and Ladd, 1954).


Kauai
S
IW
USR
S
WAILUA
USR
HW
SW
IW
S
USR
NAWILIWILI
S
S
HW
S
USR
HANAPEPE
Oahu
KAUNAKAKAI
SW
HW
S Molokai
KAHULUI
SW
HW
IW
USR
S
Maui
HANA
USR
HW
Lanai
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SW
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USR
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IW
S
KAPAAU
SW
USR
HW
IW
HW
KAWAIHAE
HILO
USR
HW
KAILUA
Hawaii
S
IW
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KAHUKU
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S
MW
IW
SW
USR
HW
S
KANEOHE
SW
S
USR
KAILUA
S
S
USR
WAIANAE
USR
S
PEARL HARBOR
HONOLULU HARBOR
DIAMOND HEAD
BARBERS PT.
MW
IW
SW
MW
HW
USR
IW
S
USR
S
USR
S
SW on occasion
LEGEND
SW—SEWAGE
MW—MILITARY WASTE
IW—INDUSTRIAL WASTE
HW—HARBOR WASTE
USR—URBAN STORM WATER RUNOFF
S—SOIL

Fig. 37. Pollutional influence around the Hawaiian Islands with particular reference to the Island of Oahu. (Knaefler, 1967).

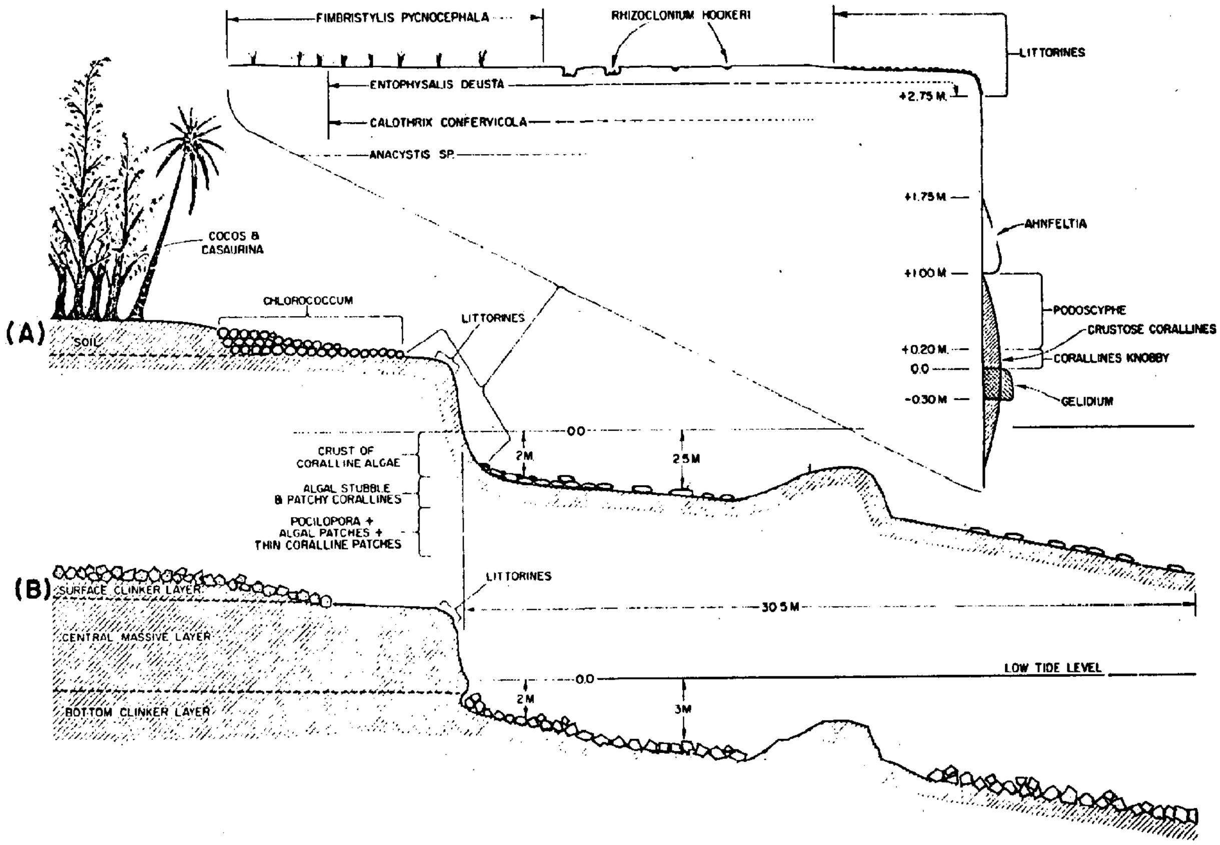
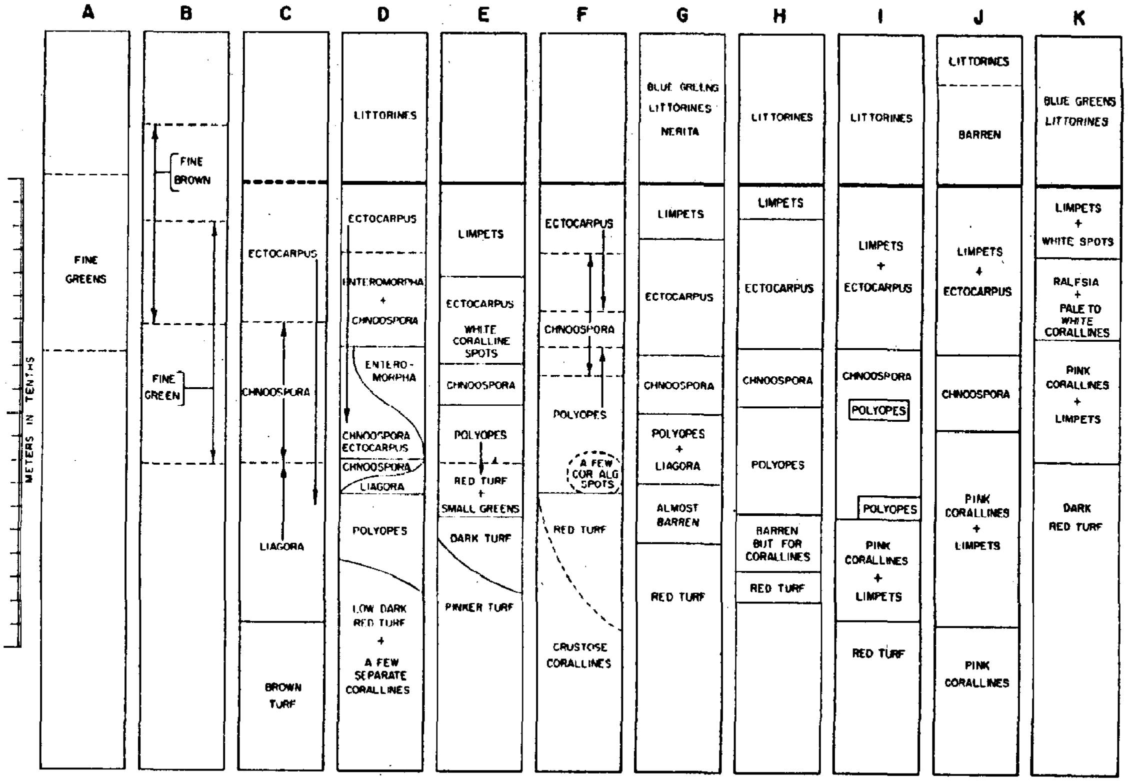
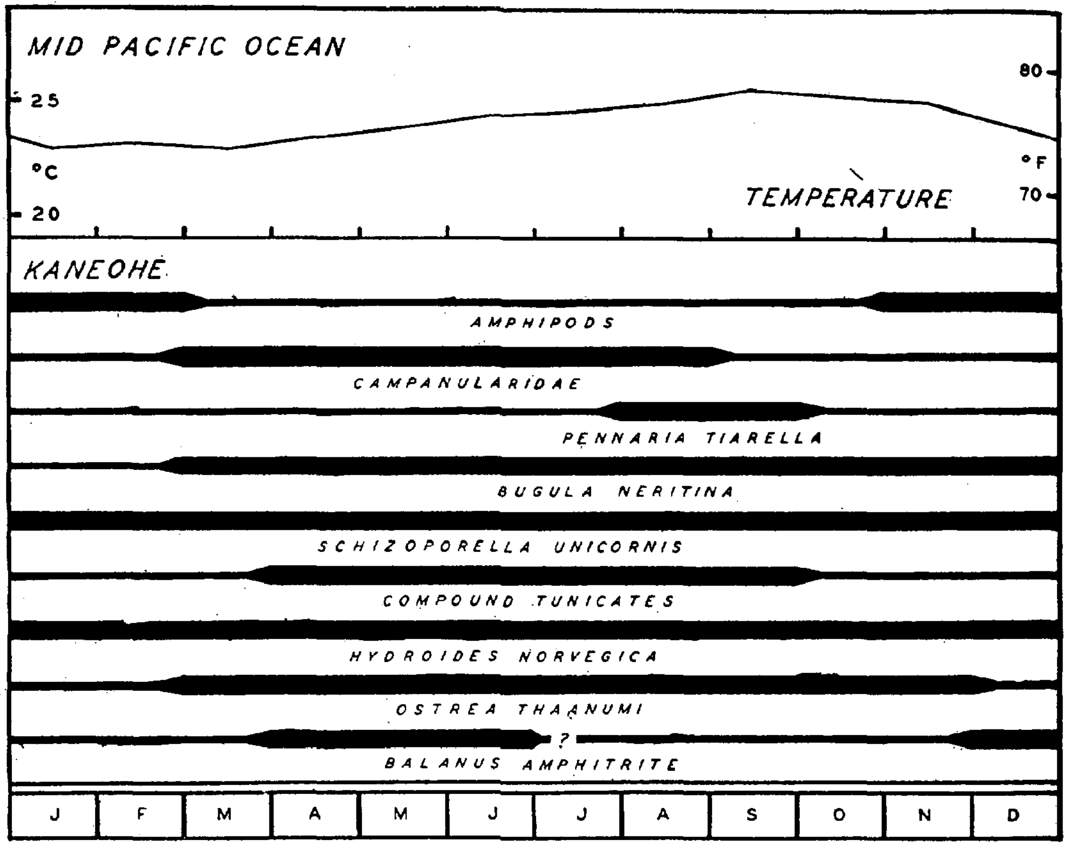

FIMBRISTYLIS PYCNOCEPHALA
RHIZOCLONIUM HOOKERI
LITTORINES
ENTOPHYSALIS DEUSTA
+2.75 M
CALOTHRIX CONFERVICOLA
ANACYSTIS SP.
+1.75 M
AHNFELTIA
COCOS & CASAURINA
+1.00 M
PODOSCYPHE
CRUSTOSE CORALLINES
+0.20 M
CORALLINES KNOBBY
0.0
-0.30 M
GELIDIUM
CHLOROCOCCUM
(A)
SOIL
LITTORINES
0.0
2M
2.5M
CRUST OF CORALLINE ALGAE
ALGAL STUBBLE & PATCHY CORALLINES
POCILOPORA + ALGAL PATCHES + THIN CORALLINE PATCHES
(B)
SURFACE CLINKER LAYER
LITTORINES
30.5 M
CENTRAL MASSIVE LAYER
LOW TIDE LEVEL
0.0
2M
3M
BOTTOM CLINKER LAYER

Fig. 38. Differences between an established shoreline and a shoreline affected by recent lava flows. This diagram represents early colonization of volcanic rock by algae (see Fig. 39) which precedes the development of a coral reef. The upper section of the diagram depicts a mature shore near Hilo, Island of Hawaii. The lower part represents shoreline affected by the new lava flows on Hawaii in 1955. (Doty, 1967 c).


A
B
C
D
E
F
G
H
I
J
K
METERS IN TENTHS
FINE GREENS
FINE BROWN
FINE GREEN
ECTOCARPUS
CHNOOSPORA
LIAGORA
BROWN TURF
LITTORINES
ECTOCARPUS
ENTEROMORPHA + CHNOOSPORA
ENTEROMORPHA
CHNOOSPORA ECTOCARPUS
CHNOOSPORA
LIAGORA
POLYOPES
LOW DARK RED TURF + A FEW SEPARATE CORALLINES
LIMPETS
ECTOCARPUS
WHITE CORALLINE SPOTS
CHNOOSPORA
POLYOPES
RED TURF + SMALL GREENS
DARK TURF
PINKER TURF
ECTOCARPUS
CHNOOSPORA
POLYOPES
A FEW COR ALG SPOTS
RED TURF
CRUSTOSE CORALLINES
BLUE GREENS
LITTORINES
NERITA
LIMPETS
ECTOCARPUS
CHNOOSPORA
POLYOPES + LIAGORA
ALMOST BARREN
RED TURF
LITTORINES
LIMPETS
ECTOCARPUS
CHNOOSPORA
POLYOPES
BARREN BUT FOR CORALLINES
RED TURF
LITTORINES
LIMPETS + ECTOCARPUS
CHNOOSPORA
POLYOPES
POLYOPES
PINK CORALLINES + LIMPETS
RED TURF
LITTORINES
BARREN
LIMPETS + ECTOCARPUS
CHNOOSPORA
PINK CORALLINES + LIMPETS
PINK CORALLINES
BLUE GREENS
LITTORINES
LIMPETS + WHITE SPOTS
RALFSIA + PALE TO WHITE CORALLINES
PINK CORALLINES + LIMPETS
DARK RED TURF

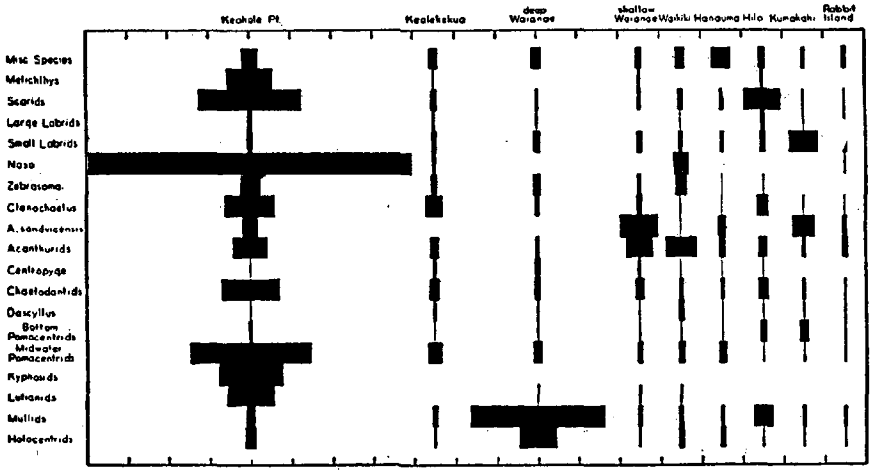
Population changes in time on a vertical 1955 lava surface extruded into the sea and observed as follows: A & C at Kaueleau (respectively), 21-VI-1955 and 15-VIII-1955; and at Kehena (respectively), B, 30-XII-1958; D, 21-XII-1955; E, 24-III-1956; F, 16-V-1956; G, 14-VII-1956; H, 18-VIII-1956; I, 10-XI-1956; J, 20-IV-1957; K, 30-XII-1958. The base line for measurement was the top of the particular population across which on the figure a dark horizontal line is drawn. This corresponded in general with a set of recognizable physical features of the shore but the physical features changed from time to time as erosion took place.

Fig. 39. Algal colonization of a recent lava flow in Hawaii. (Doty 1967c).



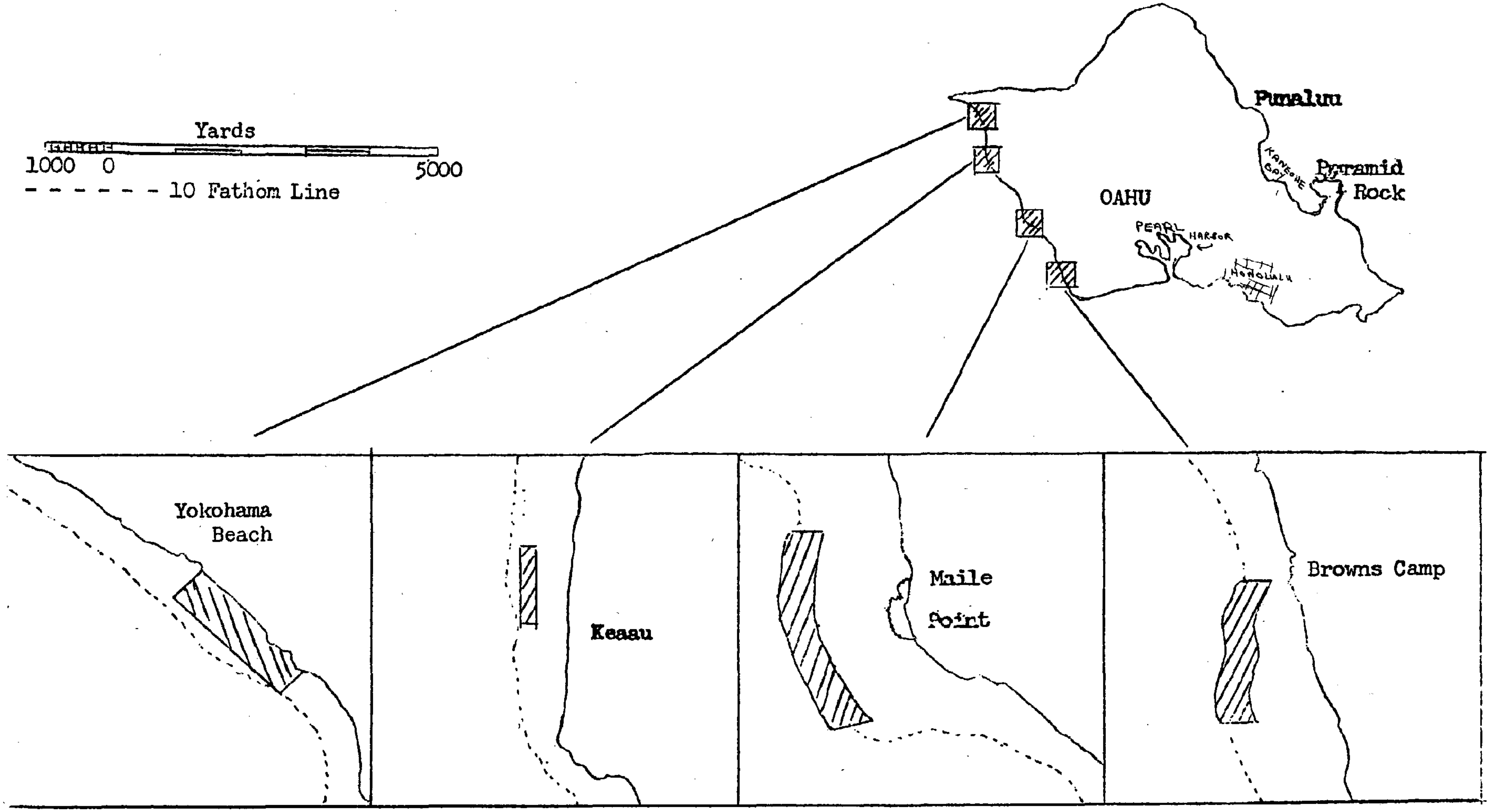
Kaneohe Bay, Oahu, Hawaiian Islands. Fouling of various materials on short and long term exposure. After Edmondson and Ingram (*6*). Temperatures: mean monthly sea surface temperatures in Hawaiian region, from Hydrographic Office, World Atlas of Sea Surface Temperatures (*15*). For additional information on fouling in Hawaiian sea, see Visscher (*41*).

Fig. 40. Fouling in Hawaii. Months other than Jan. and Feb. are favored for larval release by fouling organisms. (Woods Hole Oceanographic Inst., 1952).



Species composition by estimated weights of fishes observed along transects in nine localities around the islands of Hawaii and Oahu. Each vertical division represents 100 pounds.

Fig. 41. Quantities of fish per standard transect over Hawaiian coral reefs. Quantities of fish are related to complexity of the bottom structure. (Brock, 1954).


Yards
1000 0 5000
- - - - - - 10 Fathom Line
Punaluu
Kaneohe Bay
Pyramid Rock
OAHU
Pearl Harbor
Honolulu
Yokohama Beach
Keaau
Maile Point
Browns Camp

Station D
Shaded section = 258.3
Lbs. of fish/acre = 28.7

Station C
Shaded section = 41.3 acres
Lbs. of fish/acre = 35.4

Station B
Shaded section = 309.9 acres
Lbs. of fish/acre = 57.9

Station A
Shaded section = 206.6 acres
Lbs. of fish/acre = 100.0

Fig. 42. Standing fish crop in pounds per acre of four fishing areas along the lee coast of Oahu. These are areas of incipient reef development. (Fujimura, 1960).

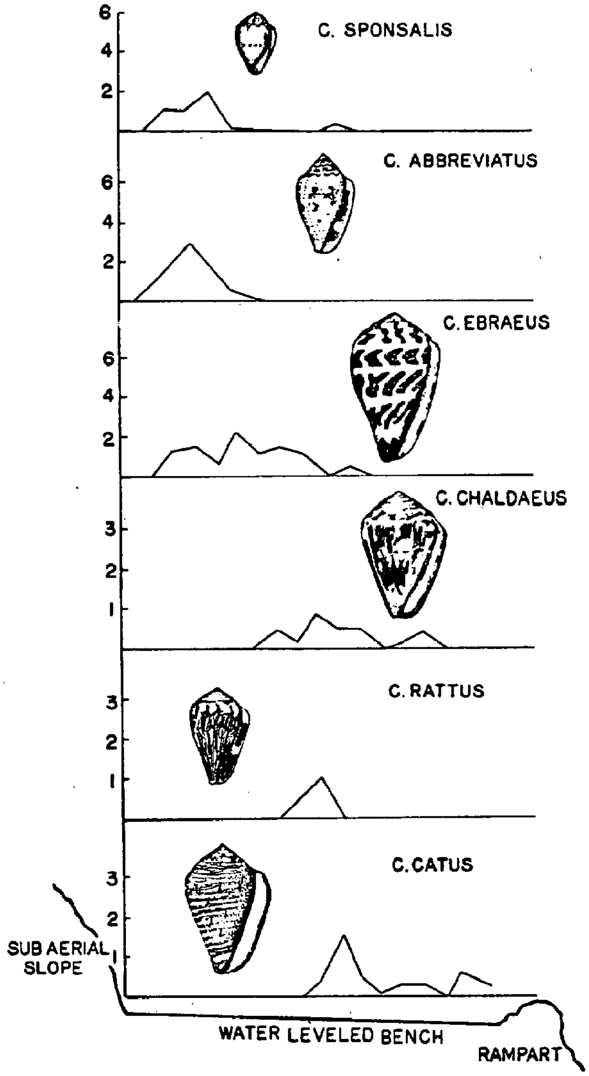


Fig. 43. The species of Conus inhabiting a wave-cut littoral bench in Hawaii, with the distribution of individuals along a transect from the landward to the seaward edge. (Hutchinson, 1965; after Kohn, 1959).

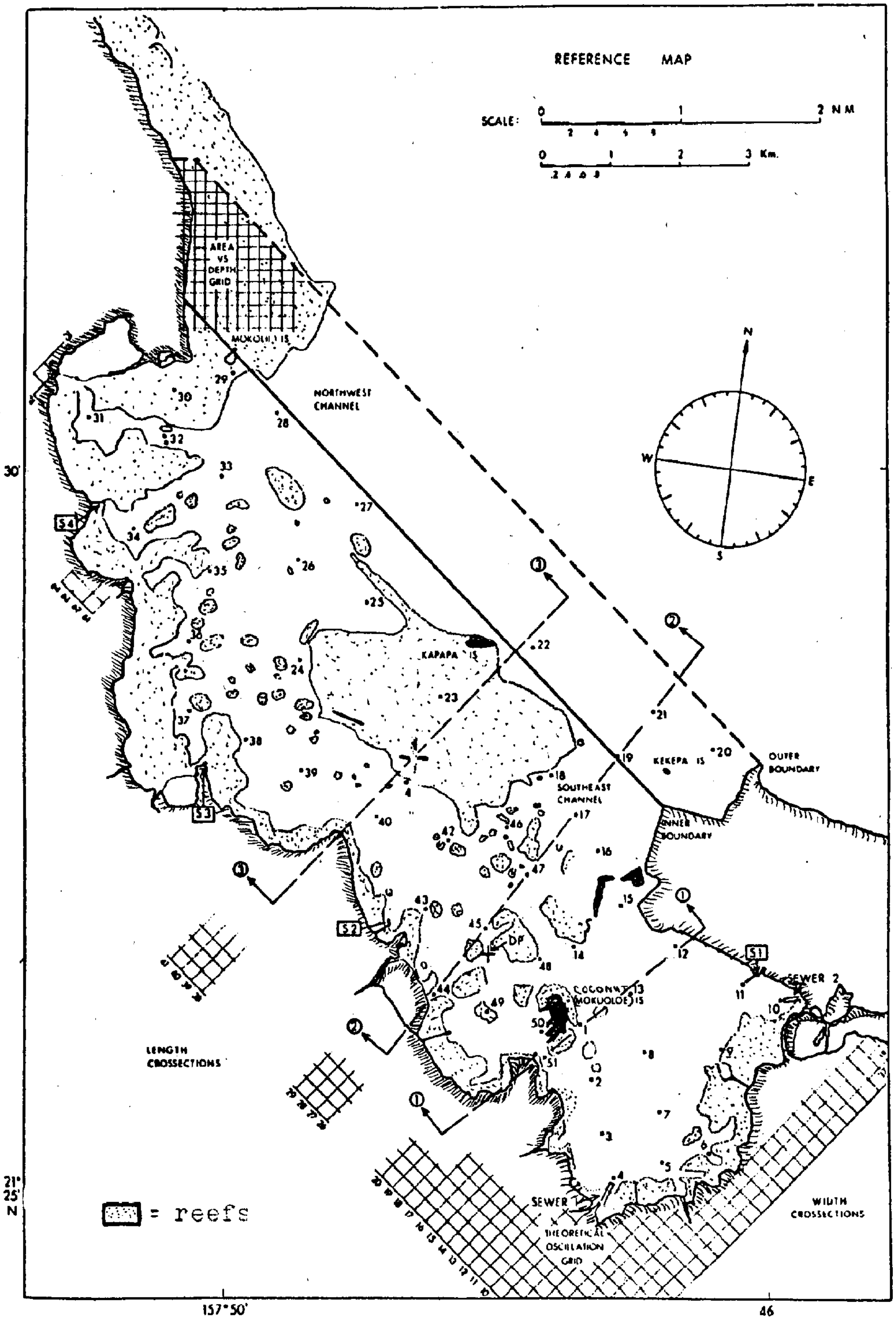

REFERENCE MAP
SCALE:
0
1
2 N M
0
1
2
3 Km.
N
S
E
W
AREA VS DEPTH GRID
MOKOLII IS
NORTHWEST CHANNEL
KAPAPA IS
KEKEPA IS
OUTER BOUNDARY
INNER BOUNDARY
SOUTHEAST CHANNEL
COCONUT (MOKUOLOE) IS
DP
SEWER 2
SEWER 1
THEORETICAL OSCILLATION GRID
LENGTH CROSSECTIONS
WIDTH CROSSECTIONS
S1
S2
S3
S4
30'
21° 25' N
157°50'
46
▨ = reefs

Fig. 44. Kaneohe Bay, Oahu, Hawaii. The barrier reef is the large formation at the mouth of the bay, occupied by Kapapa Island. Two channels connect with inner bay regions. Coral reef knolls dot the inner bay, and fringing reefs occur around the lands edge of the bay. (Bathen, 1968).

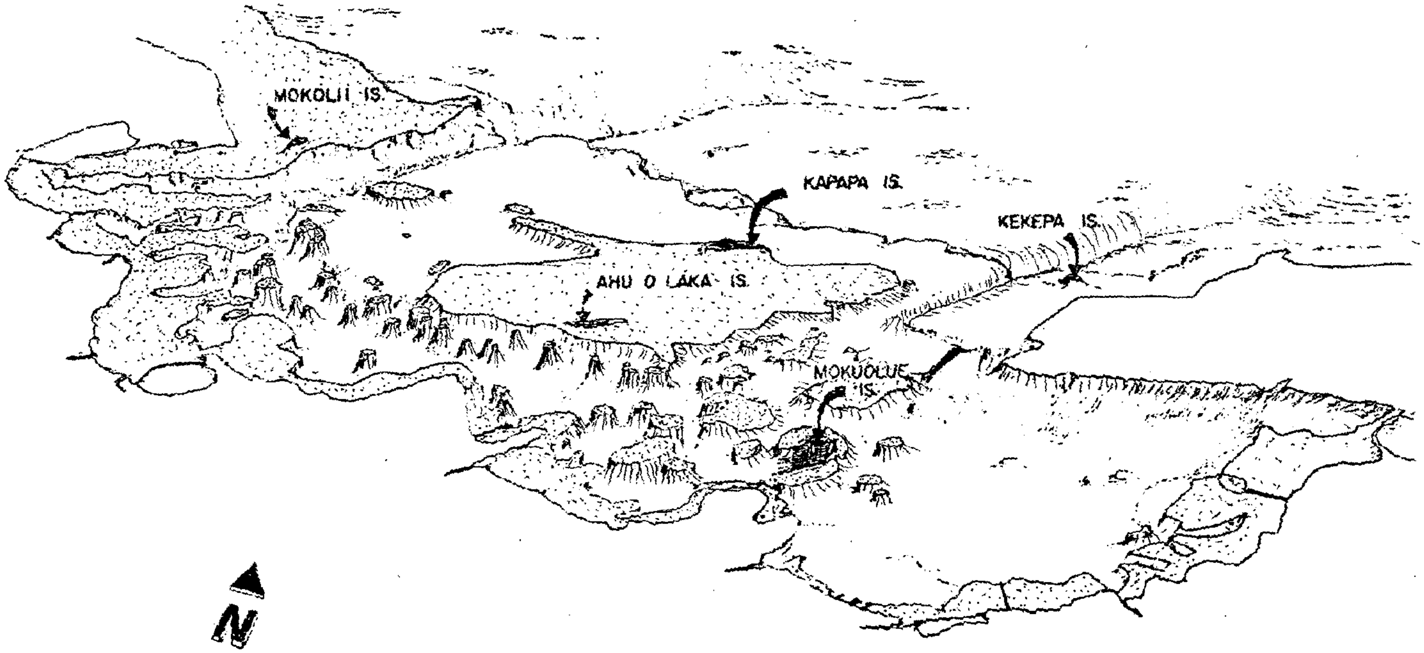

MOKOLII IS.
KAPAPA IS.
KEKEPA IS.
AHU O LAKA IS.
MOKUOLUE IS.
N

Fig. 45. Perspective view of Kaneohe Bay showing barrier reef, coral knolls, and fringing reefs. Water is hypothetically removed from the bay. (Bathen, 1968).

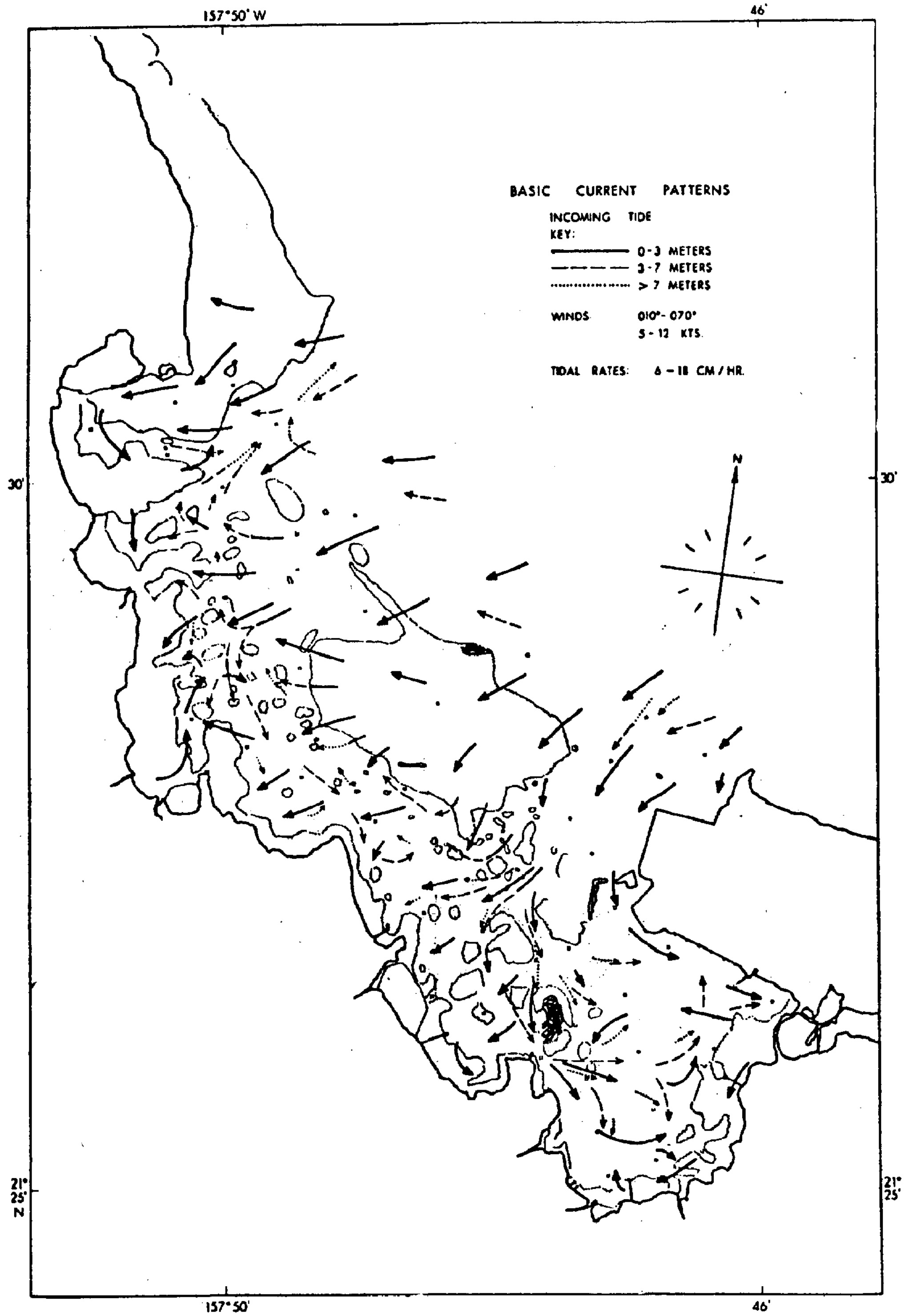

157°50' W
46'
BASIC CURRENT PATTERNS
INCOMING TIDE
KEY:
0-3 METERS
3-7 METERS
> 7 METERS
WINDS 010°- 070°
5-12 KTS.
TIDAL RATES: 6 – 18 CM / HR.
N
30'
30'
21° 25' N
21° 25'
157°50'
46'

Fig. 46. Basic current patterns in Kaneohe Bay during an incoming tide. Wind, wave, and tide driven currents come across the barrier reef, causing deep outward moving currents at the north end of the bay. (Bathen, 1968).

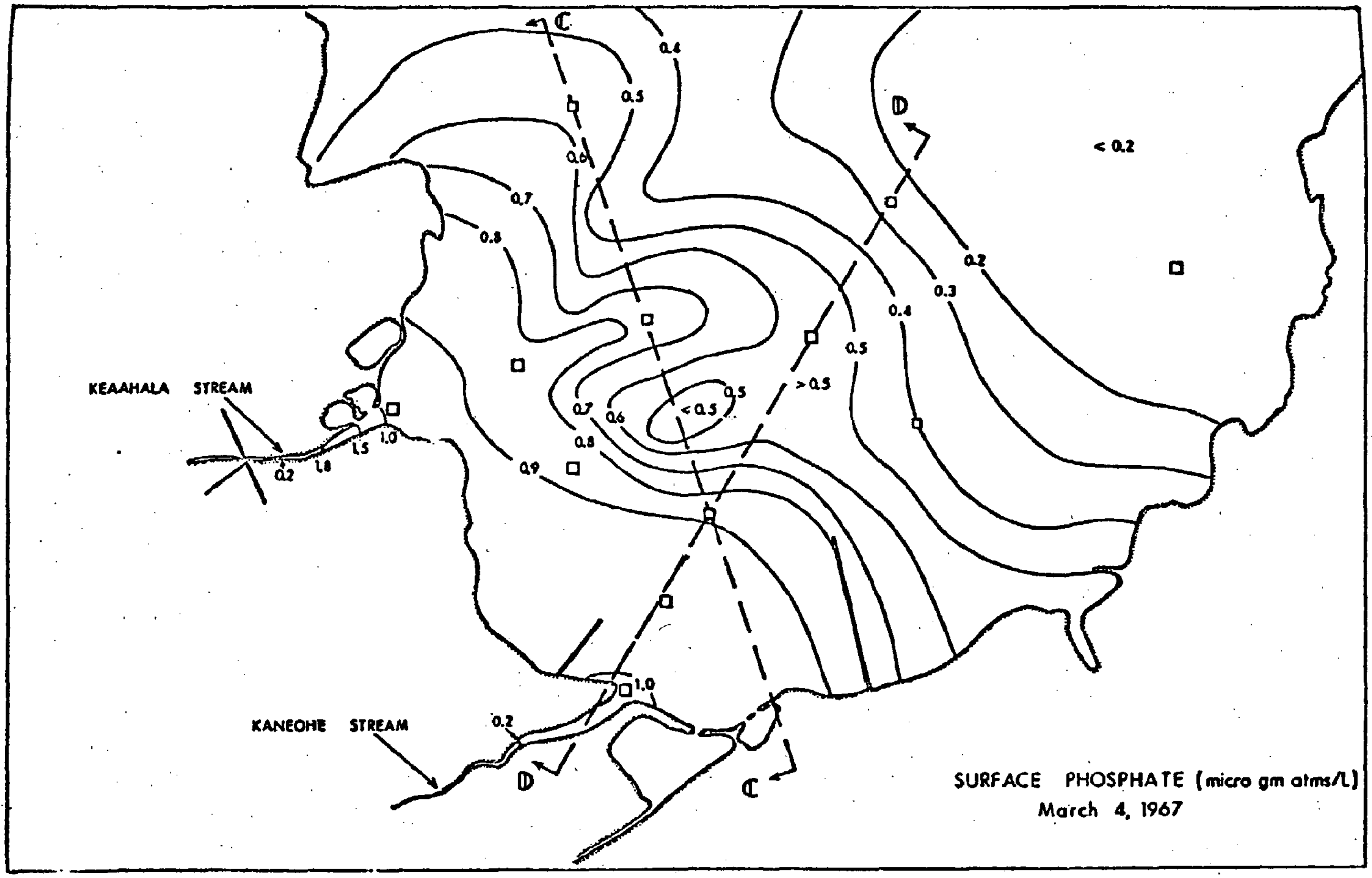

C
0.4
0.5
0.6
0.7
0.8
D
< 0.2
0.2
0.3
0.4
0.5
>0.5
0.5
<0.5
0.7
0.6
0.8
0.9
KEAAHALA STREAM
0.2
1.8
1.5
1.0
KANEOHE STREAM
0.2
1.0
D
C
SURFACE PHOSPHATE (micro gm atms/L)
March 4, 1967

Fig. 47. The southeast basin of Kaneohe Bay which receives sewage outfalls. Typical phosphate (reactive phosphorus) distribution on the surface on March 4, 1967. (Bathen, 1968).

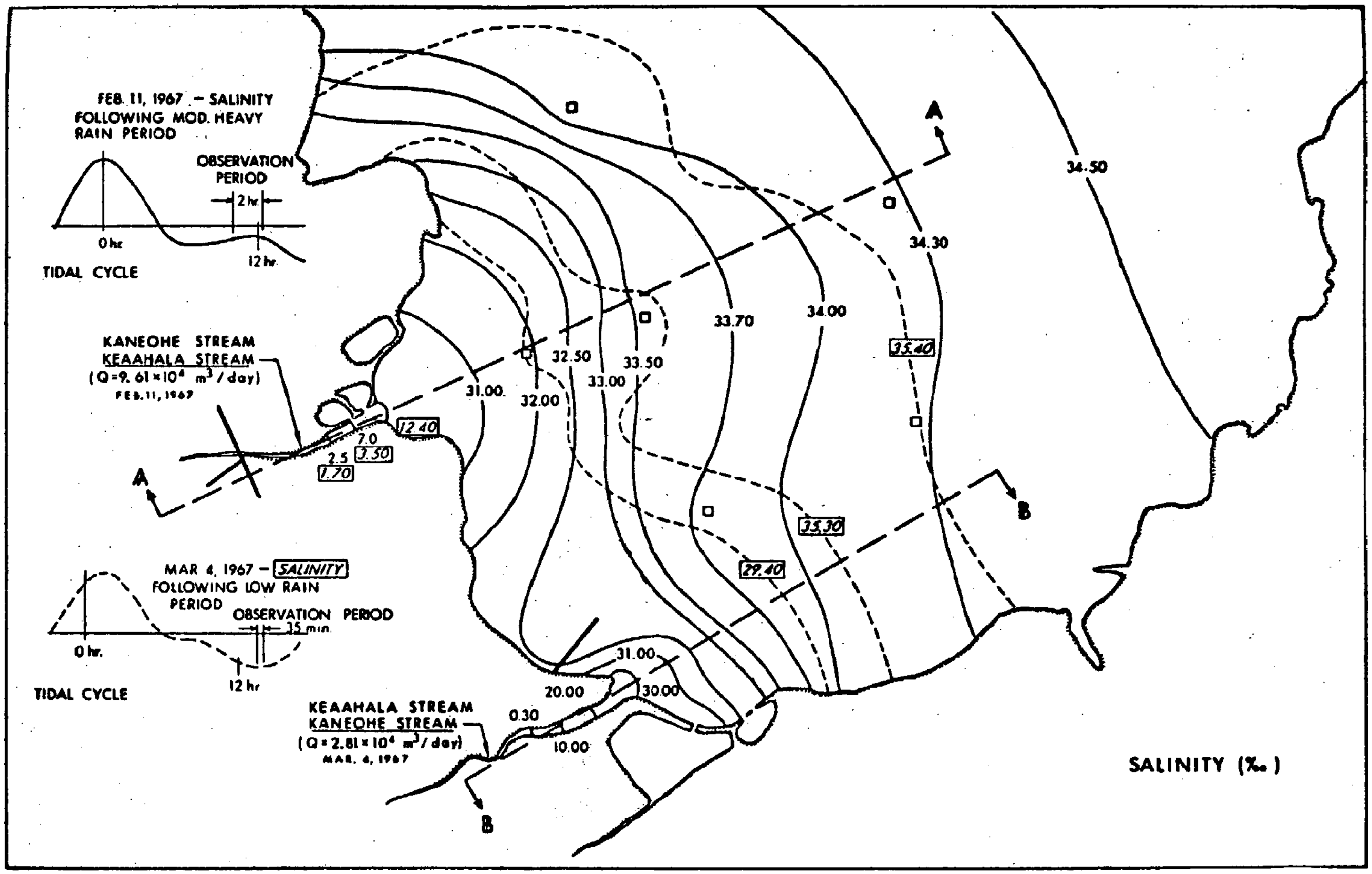

FEB. 11, 1967 – SALINITY
FOLLOWING MOD. HEAVY
RAIN PERIOD
OBSERVATION
PERIOD
2 hr
0 hr
12 hr
TIDAL CYCLE
KANEOHE STREAM
KEAAHALA STREAM
(Q=9.61×10⁴ m³/day)
FEB. 11, 1967
A
A
MAR 4, 1967 – SALINITY
FOLLOWING LOW RAIN
PERIOD
OBSERVATION PERIOD
35 min.
0 hr.
12 hr
TIDAL CYCLE
KEAAHALA STREAM
KANEOHE STREAM
(Q=2.81×10⁴ m³/day)
MAR. 4, 1967
B
B
7.0
2.5
3.50
1.70
12.40
31.00
32.00
32.50
33.00
33.50
33.70
34.00
34.30
34.50
35.40
35.30
29.40
31.00
30.00
20.00
0.30
10.00
SALINITY (‰)

Fig. 48. Southeast basin, Kaneohe Bay. Stream outflow and salinity (surface). Isohalines are shown for Feb. 11, 1967 (solid) and Mar. 4, 1967 (dotted). (Bathen, 1968).

Table 7. Water transparency in Kaneohe Bay (secchi disc) from Aug. 1963 to July 1964. (Piyankarnchana, 1965).

Month	Extinction Coefficient Line I	Line II	Line III
August	0.327	0.369	0.369
September	0.252	0.243	0.500
October	0.266	0.293	0.567
November	0.369	0.293	0.395
December	0.215	0.224	0.266
January	0.395	0.395	0.708
February	0.254	0.266	0.347
March	0.254	0.309	0.425
April	0.369	0.425	0.472
May	0.425	0.500	0.630
June	0.266	0.347	0.630
July	0.395	0.500	0.809

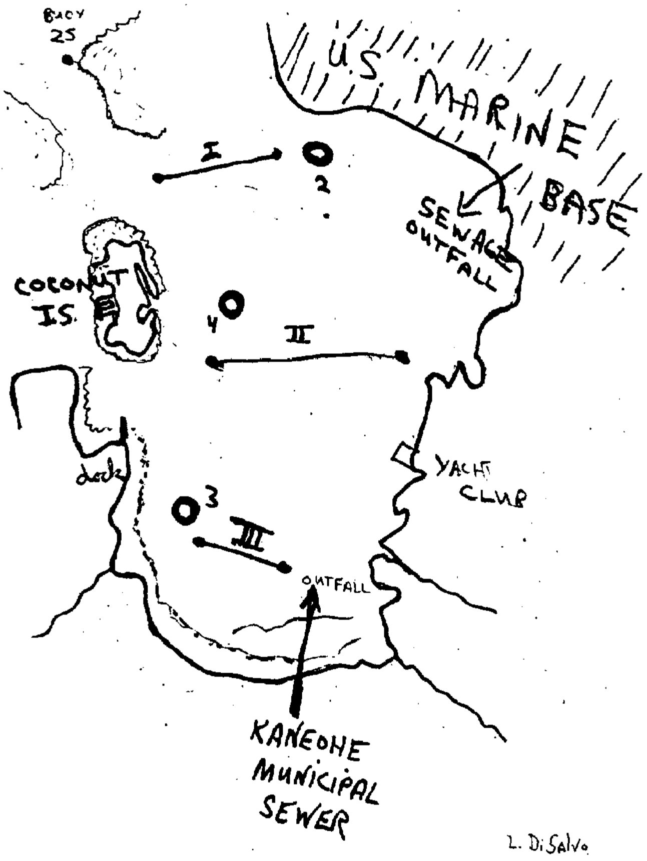


Fig. 49. Locator map, Kaneohe Bay SE basin, for Tables 7 and 8. (modified from Piyankarnchana, 1965; and Gundersen and Stroupe, 1967).

Table 8. Transparency (secchi disc) and pH values for Kaneohe Bay waters. Stations 2-4 on locator map, 5 is in middle sector of the bay, and 1 and 6 are oceanic stations outside the bay. (Gundersen and Stroupe, 1967).

STATION		pH RANGE	 AVERAGE	TRANSPARENCY (M) RANGE	 AVERAGE	EXTINCTION COEFFICIENT
1	SURFACE	8.0-8.2	8.1	6.0-13.5	11.5	0.15
	BOTTOM	7.1-8.1	7.6			
2	SURFACE	7.5-8.1	7.9	3.0-7.0	4.7	0.36
	BOTTOM	7.0-8.1	7.6			
3	SURFACE	7.8-8.1	8.0	2.0-3.5	2.5	0.43
	BOTTOM	7.4-8.2	7.9			
4	SURFACE	8.1-8.1	8.1	4.5-5.5	5.2	0.33
	BOTTOM	8.1-8.1	8.1			
5	SURFACE	8.1-8.2	8.2	8.0-10.5	8.8	0.19
	BOTTOM	8.0-8.1	8.1			
6	SURFACE	8.1-8.2	8.2	12.5-18.0	15.3	0.11
	BOTTOM	8.0-8.2	8.1			

and 51) as discussed below in the section on stress. The influence of man cannot be denied, however, with increasing inputs of poorly treated sewage wastes and increasingly diffuse and silt-laden freshwater runoff due to suburban construction. Fig. 37 illustrates the extent of pollution on Oahu as visualized by newspaper reporter Tomi Knaefler (1967). Clutter (1968) found phytoplankton and zooplankton concentrations higher in the corner of the bay receiving wastes.

Bermuda

Lying 600 miles off the coast of North Carolina in the Gulf Stream, the island of Bermuda and its surrounding reefs (Fig. 52) represents the northernmost extension of coral reefs. Bermuda is structured somewhat like a Pacific atoll in that its reefs enclose a shallow central lagoon. The reef fauna include hardy Caribbean varieties, and many species are maintained by larval importation on warm Gulf Stream currents.

Several studies of importance to the understanding of reefs have been carried out at Bermuda. Fig. 52 (inset) shows the small reef surveyed by Bardach (1959) for fish population. He found 490 kg. of fish per hectare (49 g/m^2) of which 30-40% was cited as being replacement growth. Representative data are given in Table 9. Fig. 53 from Neumann's (1966) study in Bermuda illustrates the importance of boring (clionid) sponges in the breakdown of limestone coastlines. This regeneration process is important on all reefs of the world in maintaining the balance of calcium and carbonate ions in seawater.

DISCUSSION

Reef Structure and Zonation

Reefs generally consist of a porous limestone framework gradually filled with calcareous reef sediments and cemented together by encrusting calcareous organisms. Lower regions of the reef are ultimately consolidated into a solid basement limestone by processes known as diagenesis, as yet poorly defined.

Goreau (1961) emphasizes the fact that maximum accretion of calcareous matter occurs near the turbulent surface waters where mechanical and chemical erosion processes are paradoxically at a maximum. Variously originating components have evolved a coherent structure adapted for maximum attenuation of wave stress, yet exposing maximum surface areas for biological functioning.

The skeletons of coral colonies produce the primary reef framework (Goreau, 1963). Most coral colonies consist of hundreds of tiny polyps interconnected by a thin sheet of tissue. The polyps continuously reproduce asexually at the colony surface causing expansive growth by secreting their skeletal cups of aragonitic limestone. Separate colonies may interlock by contiguous growth or may be cemented into larger framework units by encrusting coralline algae. Spaces within smaller framework units, as well as large

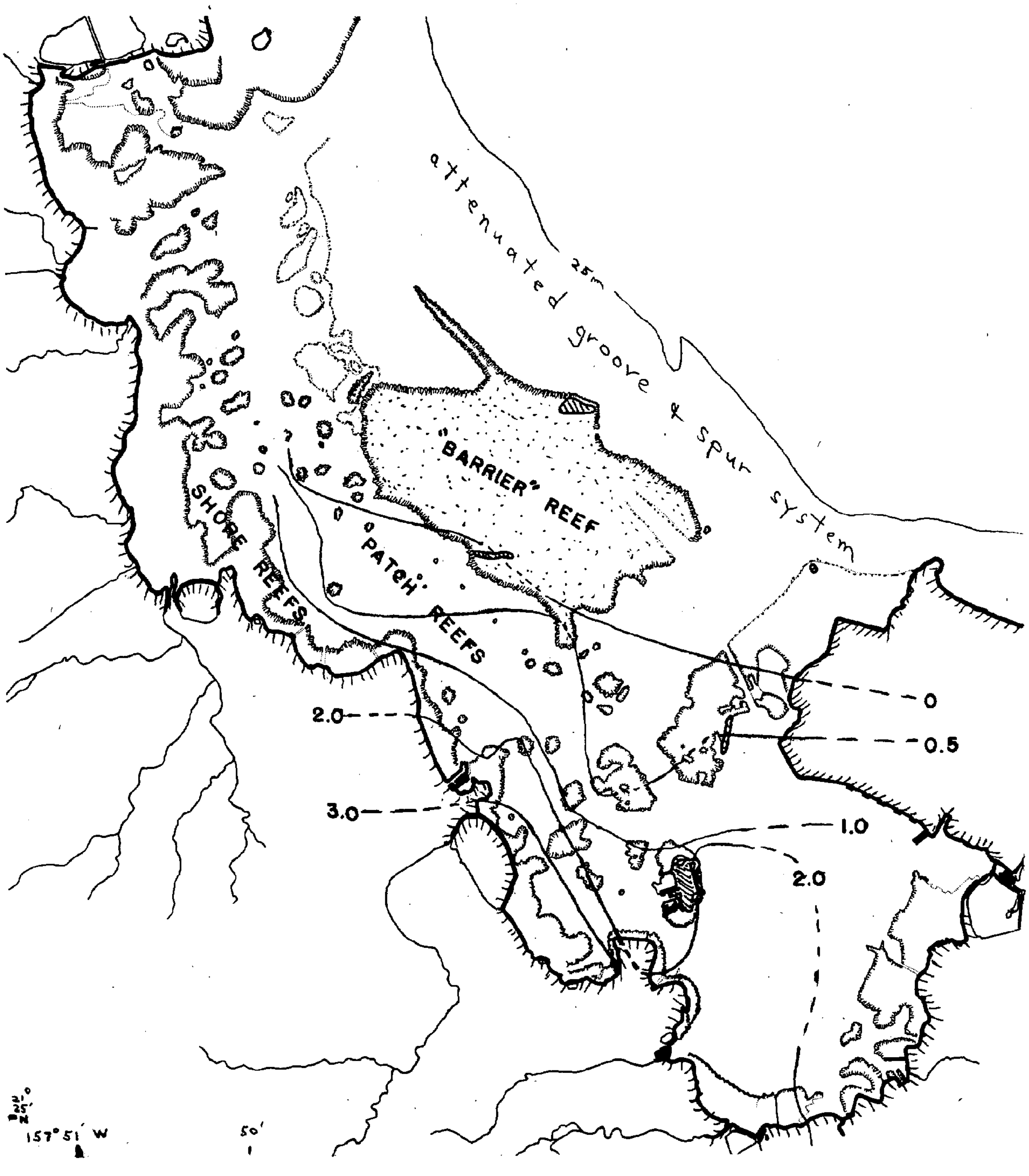

attenuated groove & spur system
25m
"BARRIER" REEF
SHORE REEFS
PATCH REEFS
0
0.5
1.0
2.0
2.0
3.0
21° 25' N
157° 51' W
50'

Fig. 50. Kaneohe Bay, Oahu, Hawaii. Lines represent "isonekros" given by Banner (unpub.) to indicate depths in meters in which corals were killed during May 1965 catastrophe. (A.H.Banner,Univ.of Hawaii,unpub.ms.)

Coincident heavy rains and reef kill , 1965 .

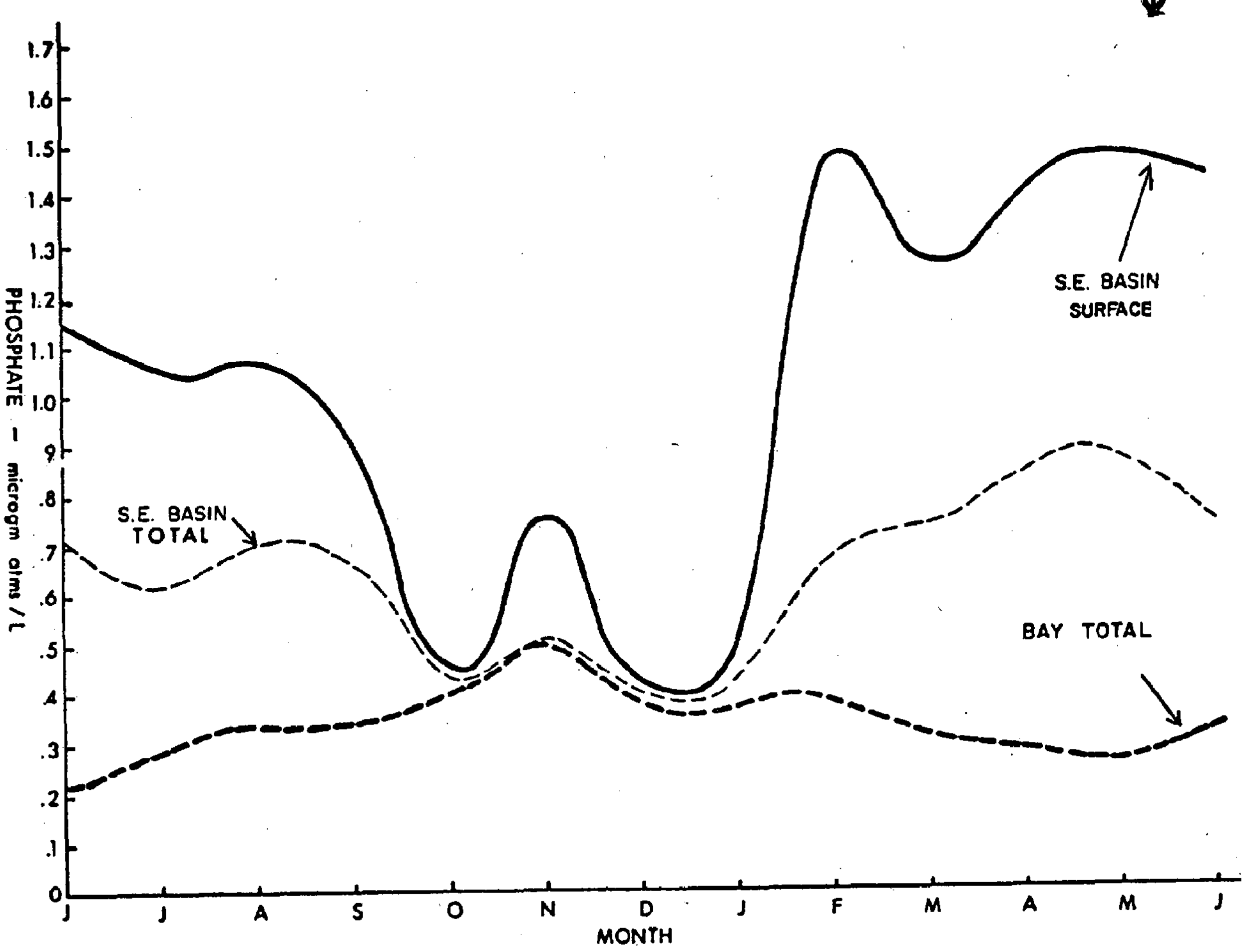
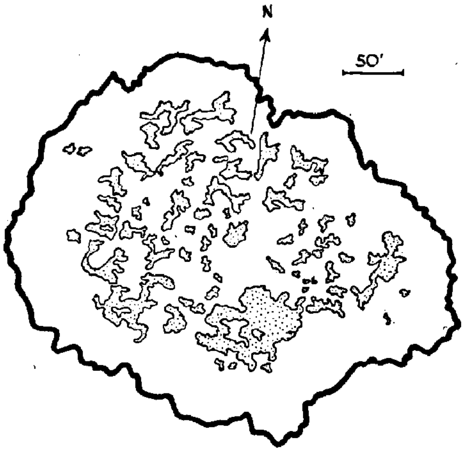
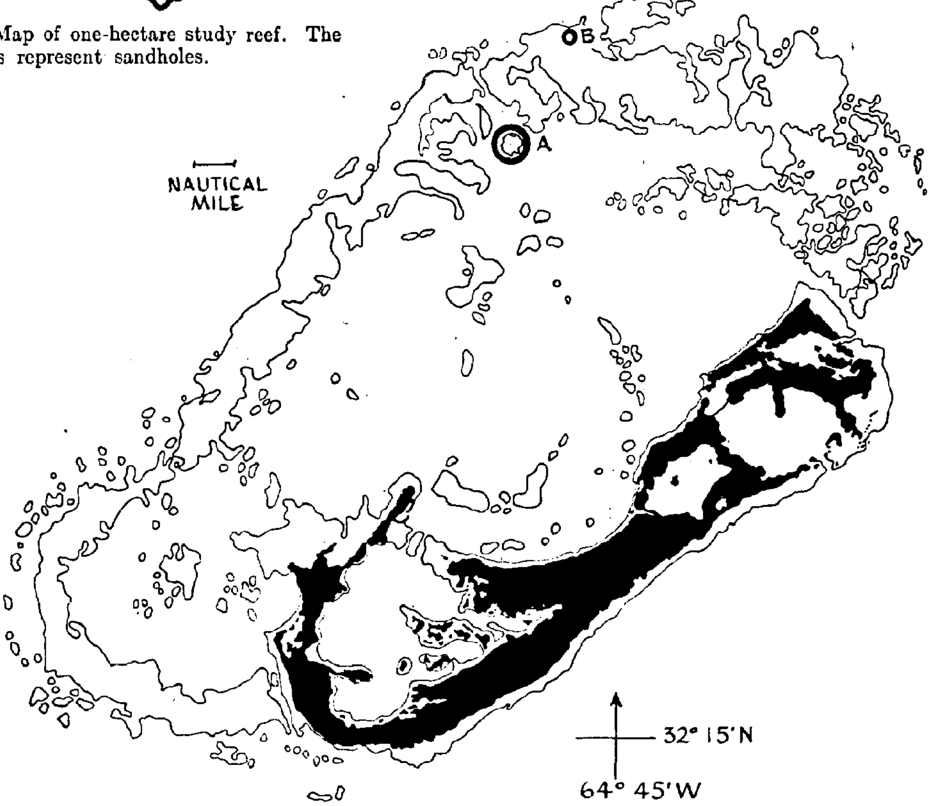


Fig. 51. Reactive Phosphorus in Microgm atms/l - Bay Total, Southeast Basin Total, and Southeast Basin surface. "Total" curves are the mean values for the entire water column and the "surface" curve is for the top ½ meter of water. (Bathen, 1968).



Map of one-hectare study reef. The dotted areas represent sandholes.



Map of Bermuda islands and surrounding reefs. *A*. Location of one hectare study reef. *B*. Location of study area on extended reef surface.

Fig. 52. Bermuda and surrounding reefs. The structure of Bermuda suggests comparison with Pacific atolls, with its' ring of reefs surrounding a relatively shallow central "lagoon". (Bardach, 1959).

Table 9. Standing crop of fishes on a one-hectare reef in Burmuda as illustrated in Fig. 52 (From Bardach 1959).

Fishes[1]	Numbers of individuals (and their estimated total weight, in kg)						Av. wt. kg/ha
	1955		1956		1957		
	No.	Wt.	No.	Wt.	No.	Wt.	
Omnivores (mostly herbivorous)							
Angelfish							
Holacanthus bermudensis (250)	82	20.5	47	11.8	45	11.3	14.5
Surgeonfish							
Acanthurus sp. (200)	150	30.8	27	5.4	18	3.6	13.3
Parrotfishes							
Adult *Scarus* and *Sparisoma* sp. (1000)	46	46.0	46	46.0	50	50.0	47.3
Subtotals, omnivores[2]		97.3		63.2		64.9	
Juvenile *Scarus* and *Sparisoma* (350)	70	24.5	—	—	—	—	24.5
Misc. small fish							
Young surgeon and parrotfish pomacentrids, etc. (10)	7000	70.0	4200	42.0	—	—	56.0
Total weight, omnivores							155.6
Carnivores							
Red hind							
Epinephelus guttatus (600)	63	37.8	24	14.4	42	25.2	25.8
Nassau grouper							
Epinephelus striatus (1115)	9	10.0	9	10.0	12	13.4	11.3
Other groupers							
Mycteroperca sp. (1500)	12	18.0	10	15.0	12	18.0	16.0
Coney							
Cephalopholis fulvus (400)	15	6.0	3	1.2	3	1.2	2.8
Grey snapper							
Lutjanus griseus (1000)	82	82.0	78	78.0	81	81.0	80.3
Bluestriped grunt							
Haemulon sciurus (400)	226	90.4	353	141.2	250	100.0	110.5
Porgy							
Calamus sp. (750)	3	2.3	1	0.8	6	4.5	2.5
Puddingwife							
Halichoeres radiatus (300)	4	1.2	2	0.6	1	0.3	0.7
Spanish hogfish							
Bodianus rufus (200)	24	4.8	15	3.0	25	5.0	4.3
Hogfish							
Lachnolaimus maximus (3000)	6	18.0	3	9.0	2	6.0	11.0
Subtotals, carnivores[2]		270.5		273.2		254.6	
Subtotals, omnivores and carnivores[2]		367.8		336.4		318.5	
Moray							
Gymnothorax sp. (400)	—	—	24	9.6	—	—	9.6
Small wrasses							
Thalassoma bifasciatum and *Halichoeres* sp. (10)	3200	32.0	4000	40.0	—	—	36.0

Table 9 (continued)

Fishes[1]	Numbers of individuals (and their estimated total weight, in kg)						Av. wt. kg/ha
	1955		1956		1957		
	No.	Wt.	No.	Wt.	No.	Wt.	
Small nocturnal and crepuscular fishes							
Holocentrus sp., *Apogon* sp. *Blenniidae* etc. (20)	—	—	1200	24.0	—	—	24.0
Total weight carnivores							334.8
Grand total weight							490.4

---

[1] Figures in brackets under species names give average individual weights of fish in grams.

[2] Subtotals of omnivore or carnivore species respectively for which three separate counts were made.

[3] Subtotals of all species for which three separate counts were made.

Occurrence of certain species of reef fishes on an extended reef near Bermuda, summer 1957, as counted by two divers, M and B

Fishes	Date of Count									
	June 14		June 20		June 26		July 16		Aug. 19	Sept. 6
	M	B	M	B	M	B	M	B	M	M
	Omnivores									
Parrotfishes										
Scarus	9	9	13	15	23	23	29	35	47	39
Sparisoma	9	6	27	12	33	19	28	20	27	22
Angelfish										
Holacanthus	—	—	14	15	14	14	18	19	25	20
Surgeon fish										
Acanthurus	11	4	30	21	20	14	21	18	33	28
	Carnivores									
Red Hind										
Epinephelus guttatus	—	—	—	1	2	2	1	1	—	1
Groupers										
Mycteroperca sp.	—	—	—	1	—	1	—	1	—	—
Coney										
Cephalopholis fulvus	—	—	2	—	—	5	1	1	3	2
Grunts										
Haemulon sp.	3	3	1	2	4	2	5	5	2	4
Grey snappers										
Lutjanus griseus	3	—	—	1	—	—	—	—	—	—
Puddingwife										
Halichoeres radiatus	2	—	2	2	2	2	2	3	—	—
Others	—	—	9	7	5 (Barracuda)	4	3 (School of jacks, 50+, seen by both)	3	3	9

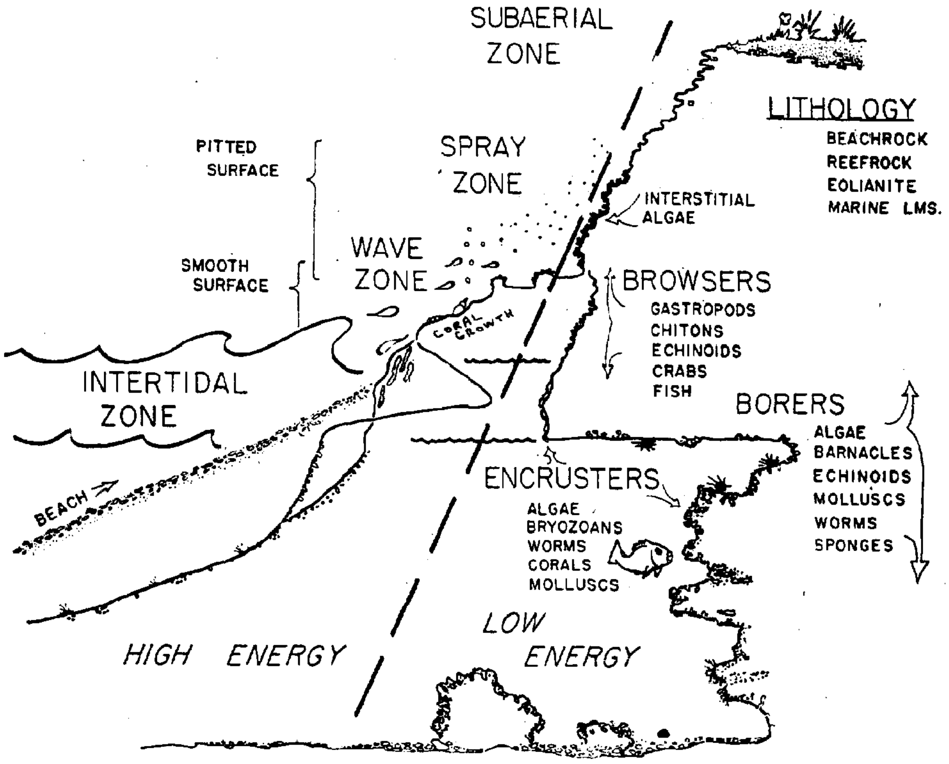

SUBAERIAL ZONE
LITHOLOGY
BEACHROCK
REEFROCK
EOLIANITE
MARINE LMS.
PITTED SURFACE
SPRAY ZONE
INTERSTITIAL ALGAE
SMOOTH SURFACE
WAVE ZONE
BROWSERS
GASTROPODS
CHITONS
ECHINOIDS
CRABS
FISH
CORAL GROWTH
INTERTIDAL ZONE
BORERS
ALGAE
BARNACLES
ECHINOIDS
MOLLUSCS
WORMS
SPONGES
BEACH
ENCRUSTERS
ALGAE
BRYOZOANS
WORMS
CORALS
MOLLUSCS
HIGH ENERGY
LOW ENERGY

Illustration of the general coastal morphology and zonation observed at Bermuda including notation of biological agents and processes associated with coastal erosion.

Fig. 53. Coastal erosion in Bermuda. Sand formation and the return of calcium and carbonate ions to seawater are accomplished by macro-and microscopic processes of limestone breakdown. (Neumann, 1966).

areas sequestered from the force of waves are gradually filled by transported calcareous fragments ranging in size from sands to gigantic storm-tossed boulders.

Although there are several overall differences in plant and animal species composition between Atlantic and Pacific coral reefs (Wells, 1957), reefs exposed to similar wave energies show similar geomorphological zonation. Fig. 1 depicts the general morphology of a Jamican reef which has similarities to other Caribbean reefs but is among the best developed with regard to complexity of zonation and species of coral. Some of the zones in Figs. 1 and 36 may be described as follows.

The inshore reef flats are inhabited by physiologically hardy varieties of animals and plants which can withstand stresses caused by temperature and salinity fluctuations.

The channel, or lagoon region is a sandy back reef zone seen in various forms on many of the world's coral reefs. These are usually quiet waters which receive calcareous sediments produced on other regions of the reef. An active foraminiferan population may produce sand. As mentioned above, in areas of high temperature and slight water movement calcium carbonate may be directly precipitated from seawater. Turtlegrass beds commonly found on Atlantic reefs are less common on the Indo-Pacific reefs, and are usually replaced in those regions by calcareous algae such as Halimeda. Back-reef coral zones are typically very diverse, in the absence of limiting stress, and are usually chosen for popular magazine articles as representative of coral reefs. Where lagoons exist, deeper lagoonward zones may show luxuriant coral growth with corals expressing their most typical growth forms. Large formations in these areas are often interspersed with reef sands. Large fish populations are often seen grazing in these areas. Shallower coral flats, exposed or nearly so at low tide, are populated by species of low spreading corals or adaptive forms of species also found in deeper waters. These exposed flats often become decadent areas when upward growth and low tide combine to cause fatal exposures to air and sunlight. Sedimentation on these sites makes them amenable to colonization by coconut palms or mangroves with eventual island formation under favorable conditions.

The buttress zone is a region of the reef which grows outward against the forces of the ocean. Coral growth forms show protective orientation with respect to waves, and selection is for the sturdy species. Invertebrates living in these regions are usually small and well adapted for holding onto the substratum. As the buttress system gives way to deeper waters more fragile corals appear, and coral growth gradually thins out as light becomes limiting. Sediments broken from the reef front are either washed over the reef into the back reef zones or deposited down the front face of the reef as a "talus slope".

The major difference between fully wave-exposed reefs in the Indo-Pacific and those in the Atlantic is the absence in the latter of a calcareous algal ridge breaking surface water at low spring tides (Yonge, 1963a). This algal ridge is formed primarily by the Melobesioid algae (eg. Porolithon) and small coral heads. Fig. 5 shows the algal ridge and buttress zone at Bikini Atoll in the Marshall Islands. This is a form typical of Pacific reefs and is related to similar structure (Fig. 23) on the Florida reef tract, Jamaica (Fig. 1), and some other wave stressed reef areas. The coral species distribution in relation to depth has been given in Figs. 6 and 26. Variations in reef morphology are seen as one travels toward the extremes of the temperature regimes of reefs. Fig. 24 shows a more simply structured reef occurring near Miami, Florida. Figs. 15 and 16 demonstrate variations in reef morphology in various localities.

Trophic Organization

The living units of reefs are arranged in a highly adaptive manner for maximum efficiency of food production, food acquisition, food consumption, and cycling of waste products. Fig.1 illustrates some faunal segments and reef representatives.

The primary producers on reefs are the ubiquitous reef algae. These algae include the encrusting and free-standing reds (Rhodophyceae), the filamentous and free standing greens (Chlorophyceae), the benthic diatoms (Bacillariophyceae), boring and encrusting bluegreen algae (Cyanophyceae), and multitudes of endosymbiotic algae (Dinophyceae), inhabiting the tissues of corals and some other invertebrates. Marsh (1968) found high primary productivity of Porolithon (a red encrusting alga, Fig. 4) and Bakus (1967) has shown high production rates for potentially nitrogen-fixing bluegreens (Calothrix, Schizothrix) growing on the Eniwetok reef flat behind the algal ridge.

Grazing, rasping, and boring animals erode the surfaces of hard substrates and chew up calcareous materials, absorbing digestible products and passing out residual matter as fecal detritus. These animals include sea urchins, crabs, errant polychaetes, boring molluscs and worms, and grazing gastropods and fishes. A large percentage of the reef animals are adapted for suspension feeding, having adaptations for precipitation of particulate and dissolved nutrient matter from seawater. These animals include the sponges, solitary and colonial tunicates, sedentary polychaete worms, barnacles, bivalve molluscs, certain crustaceans, and echinoderms. Another segment of the coral reef population is adapted for moving throughout the dead coral spaces and scavenging detrital materials with re-ingestion and re-deposition of fecal pellets. This group includes the errant polychaetes, gastropods, crabs and other crustaceans, and small fishes. Some predators on the above system include carnivorous gastropods, starfishes, polyclad flatworms, errant polychaetes, and predatory fishes.

The internal spaces of the reef frame are lined with a detrital sediment containing extensive bacterial populations (DiSalvo, in prep.). The diverse microfauna in this sediment includes nannoflagellates, diatoms, protozoa, nematodes, microcrustacea and other micro-organisms suggesting active mineralization processes associated with complex micro-community-structure (Johannes; 1965, 1968). Due to the complexity of reef biotic structure, the trophic relationships are not well documented. Hiatt and Strasburg (1960) show the ecological relationships of the fish fauna on reefs at Bikini, Arno, and Eniwetok Atolls in conjunction with nuclear testing (Fig. 32-35).

Processes

Production measurements on coral reefs based on diurnal fluctuations (Figs. 19 and 30 and Tables 1, 3 and 6) are comparable to rates measured for productive agriculture (Odum, 1959), although the community structure on the reef is such that the plant production is rapidly utilized in community maintenance. A census and measurement of biomass on the Japtan reef, Eniwetok Atoll yielded biomass pyramids depicted in Fig. 28.

Growth and accretion rates have been measured on coral reefs by several investigators. Mayer (1924) reported that the integrated vertical growth of a Samoan reef was 8 mm. (1/3 in.) a year. Edmondson,(1929) found that corals on Waikiki reef, Oahu, Hawaii grew upwards at an average rate of 13 mm. (1/2 in.) annually. Oostdam (1963) studying a reef on Maui, Hawaii, estimated the annual average production of $CaCO_3$ in the area to be about 0.32 lb. per square foot of which roughly half was reef frame and the other half sediment (preceding three citations from Moberly and Chamberlain, 1964). Rates of calcification for individual organisms are given by Goreau (1961) in Tables 10 and 11. Sandy sediments are derived from skeletal remains of calcareous algae, foraminifera, sponges, echinoderms, molluscs, arthropods, and other calcareous reef organisms. Daily activities of reef borers and scrapers result in the release of sedimentary particles from primary reef frame structures. Bardach (1961) estimated that rasping fishes re-deposited 108 g. of $CaCO_3$ per m^2 per year. The calcareous sediments of a reef can often be identified as to organismic origin and physical environment by inspection of microscopic characteristics, and are used in studying the paleoecology of reefs (Ginsburg,et al.,1963).Fig. 25 illustrates the recent distributional pattern of calcareous sediments on the Florida reef tract. Hoskin (1962) showed role of large animals in grinding skeletons.

Stress

The reef ecosystem, with its high rate of organic production and consumption and its many specialized organisms and organismic interrelationships is analogous to some terrestrial climax ecosystems such as tropical rain forests. The existence of great complexity and variability suggests in some ways the division of labor and specialization of modern human cities. The state of knowledge regarding coral reefs is developed mainly along lines of taxonomy and physiology of the component parts rather than on functioning of the system as a whole. There are as yet few measured parameters which allow us to predict the nature of reef survival, succession, and ability to sustain harvesting. As with other highly structured natural communities (or cities) a disorganizing influence applied to a vital community structure or function may prove disastrous to the entire system, the ruins of which may emerge as a new system of altered structure with changed esthetic and economic values. Coral reef stress may be defined as any abnormal occurrence which results in the breakdown of reef structure and function. This may occur directly by physical, chemical or biological alteration of the reef, or indirectly by alteration of limiting factors as presented in Fig. 11.

The stresses easiest to understand are the direct physical destructions imposed on reef structure. Alteration of limiting factors includes change in

Table 10. Specific calcification and productivity rates of reef building (hermatypic) and non reef building (ahermatypic) organisms in Jamaica. Data obtained by measurement of concomitant uptake of Ca45 and C^{14}. Specific uptake measurements relate amount of uptake to the N content of organisms studied. (Goreau, 1961).

Category	Species	Light or Dark	µg.Ca/mg.N/hr	µg.carbonate-C/mg.N/hr.	µg.organic–C/mg.N/hr.
Ahermatypic Coelenterata without Zooxanthellae	*S. roseus*	light	12.0	3.30	1.250
		dark	13.2	2.46	0.489
	A. solitaria	light	8.7	1.33	0.547
		dark	8.6	0.77	0.400
	T. tenuilamellosa	light	5.5	0.56	0.217
		dark	5.6	0.85	0.161
Hermatypic Coelenterata with Zooxanthellae	*A. cervicornis* *(apical cm.)*	light	126.3	17.93	12.090
		dark	35.1	4.09	0.861
	M. complanata	light	59.6	10.19	19.680
		dark	25.0	6.44	1.640
	P. furcata	light	26.7	8.14	13.800
		dark	5.6	0.63	0.532
Hermatypic Algae	*H. tuna*	light	178.0	23.21	26.390
		dark	77.9	9.36	0.905
	H. opuntia	light	256.1	38.46	50.520
		dark	72.6	11.82	0.899
	A. fragilissima	light	68.3	43.33	56.320
		dark	792.6	87.24	2.180

Table 11 Calcification and carbon fixation rates of hermatypic and ahermatypic organisms on a daily basis. (Goreau, 1961).

Category	Species	Calcium deposition in µg./mg.N/day	Carbon fixation in µg/mg.N/day
Ahermatypic Coelenterata without zooxanthellae	*S. roseus*	292.4	
	A. solitaria	207.6	
	T. tenuilamellosa	133.2	
Hermatypic Coelenterata with zooxanthellae	*A. cervicornis* *(apical cm.)*	1936.8	145.08
	M. complanata	1015.2	236.16
	P. furcata	387.6	165.60
Hermatypic algae	*H. tuna*	3070.8	316.70
	H. opuntia	3944.4	606.24
	A. fragilissima	10330.8	675.84

the temperature regime, salinity changes, and decrease in light penetration (turbidity) with its concomitant physically damaging sedimentation. Reduction in water circulation and wave action may also have effects. The most difficult stress to understand is the spontaneous appearance of a naturally occurring biological fluctuation.

Physical

Documentations of natural physical damage due to high wind and waves are numerous. Glynn et al. (1964) noted up to 50% demolition of reef corals on a Puerto Rican reef after the passage of hurricane Edith in 1963. Stoddart (1962) described extremely violent hurricane conditions which completely destroyed a Caribbean cay including its groove and buttress system. Widespread damage to corals of up to 80% was recorded for some tracts.

Man-induced damage has been documented by Brock et al. (1966) who discussed the effects of dredging at Johnston Atoll (Figure 54 and Tables 12 and 13). Physical damage induced by human beings, including the removal of coral souvenirs, molluscan shells, and fishes (by spearfishing) in Oahu's Hanauma Bay prompted the Hawaii legislature to convert the area into a state natural preservation area.

Temperature

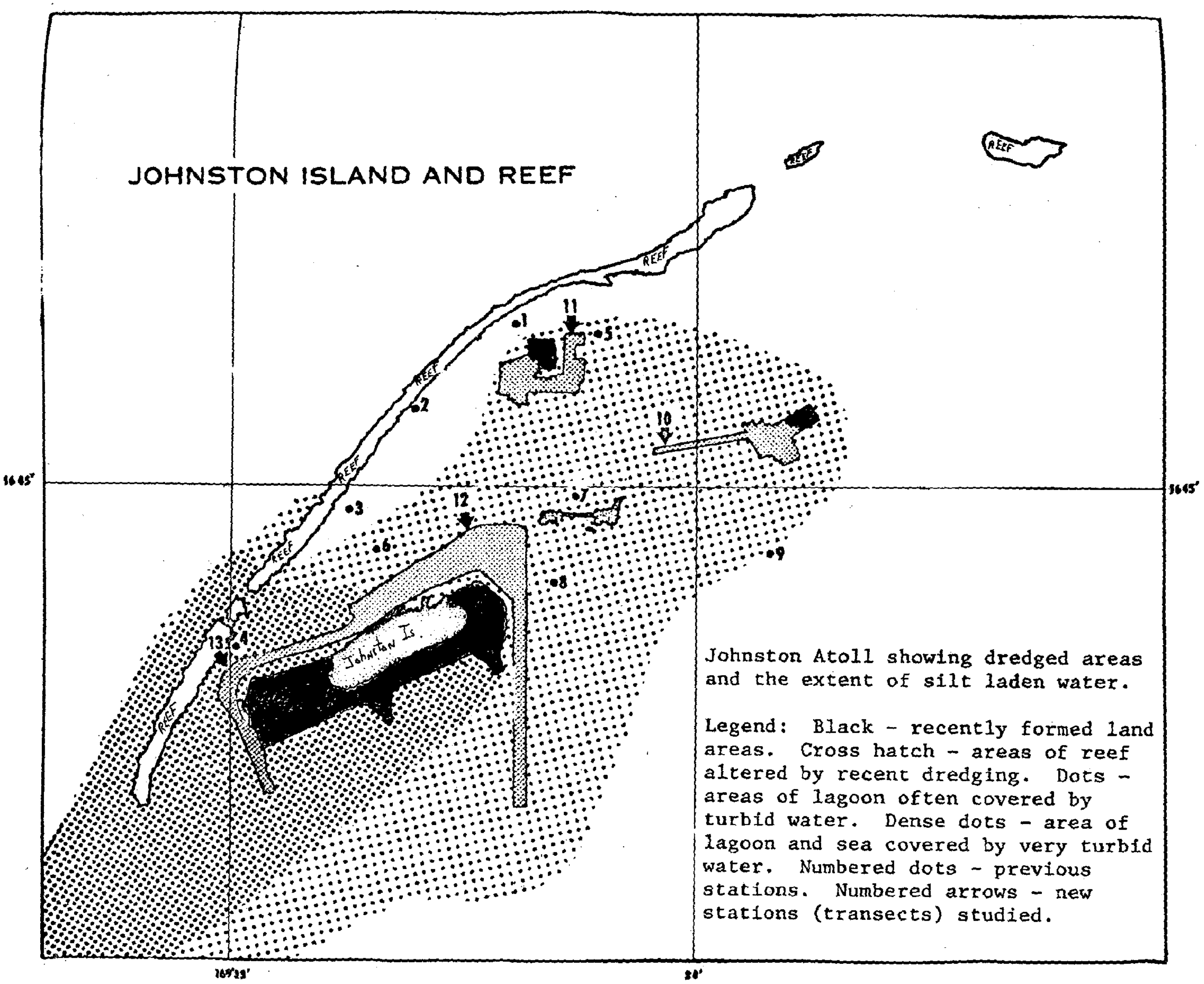
Naturally occurring mass mortalities of reef organisms have occurred as a result of their exposure to high temperatures and to air in shallow reef pools and areas exposed at extremely low tides (Mayer, 1914; Glynn, 1968). Although documentations of the catastrophes have been made, no data on long-term effects have been recorded.

There are no records of man-induced reef disturbance due to temperature stress, although proposed construction of a nuclear power plant at a site on northern Kaneohe Bay, Oahu, Hawaii may affect the normal temperature regime of coral reefs in the Bay in a region less troubled by sewage and land runoff (V. Brock, personal communication).

Salinity and Turbidity

Coral reefs most likely to be affected by catastrophe are those near high land masses which promote heavy rainfall. During periods of rainfall, freshwater inflows (perhaps laden with silt or other detritus) may cause osmotic stress to corals and other reef organisms resulting in mass mortalities. Secondary effects of the runoff are siltation and eutrophication. Siltation affects plants and sedentary animals who may not be able to clean their surfaces efficiently for continued functioning, whereas eutrophication is an enrichment effect, promoting "blooms" of microorganisms which cloud the water for days after the rainfall. These effects may be duplicated or magnified by man's introduction of municipal primary treated sewage effluents.

Banner (unpublished ms) describes the widespread reef "kill" in Kaneohe Bay, Oahu, Hawaii of May 1965 when unusual rains of nearly 18 inches fell in 25 hours, with a total rainfall of 30 inches in a ten day period.


JOHNSTON ISLAND AND REEF
REEF
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1
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10
11
12
13
16°45'
16°45'
169°33'
30'

Johnston Atoll showing dredged areas and the extent of silt laden water.

Legend: Black - recently formed land areas. Cross hatch - areas of reef altered by recent dredging. Dots - areas of lagoon often covered by turbid water. Dense dots - area of lagoon and sea covered by very turbid water. Numbered dots - previous stations. Numbered arrows - new stations (transects) studied.

Fig. 54. Johnston island and silted reef areas. See Tables 12 and 13. (Brock *et al*. 1966).

Table 12. Changes in reef echinoderm fauna as a result of dredging operations. Number of organisms found along an arbitrarily established 20 meter transect line (Brock et al 1966).

A Comparison of the Echinoderm Fauna
Inhabiting the New Stations

Echinoderms	Area 10		Area 11		Area 12		Area 13	
	Reef	Dredged area	Reef	Dredged area	Reef	Dredged area	Reef	Dredged area
Tripneustes gratilla	X			XXXX		X	XX	
Echinothrix diadema			XXX					
Echinothrix calamaris			X	X		X		X
Diadema sp.	X		XXXX	XX		X		X
Heterocentrotus mammillatus							X	
Holothuria atra				XXX				
Total No. Species	2	0	3	4	0	3	2	2

Table 13. Effects of dredging at Johnston atoll. Note reduction in percentage of living coral, reduction of echinoderm fauna, reduction in number of fish species, proliferation of algae (Brock et al 1966).

AREA 4 (Refer to map for location)

A. Fauna

1. The dominant coral genera in the area:

1964	1965
Pavona *Montipora* *Acropora* (vasiform) *Acropora* (cespitose) *Pocillopora*	Same as 1964

The estimated percent of living coral:

1964	1965
20% or less	10% to 15%

2. The conspicuous echinoderms in the area[1]:

1964

Heterocentrotus mammillatus....XXX
Tripneustes gratilla...........X

1965

Tripneustes gratilla...........X (only 2 seen)

1964	FISHES	1965
41 species		20 species

B. Flora

1. Algae collected from the top of a coral head ca. 1 meter below the surface of the water; water turbid, visibility -- minus 2 meters. August 20, 1965. Material growing largely on dead *Pocillopora*.

Greens	Browns	Reds	Blue-greens
Acetabularia	*Ectocarpus*	*Antithamnion*	*Calothrix*
Bryopsis	*Pocockiella*	*Centroceras*	*Lyngbya*
Caulerpa		*Ceramiella*	*Microcoleus*
Enteromorpha		*Ceramium*	
		Goniolithon	
		Griffithsia	
		Herposiphonia	
		Hydrolithon	
		Hypnea	
		Jania	
		Peyssonelia	
		Wurdemania	

C. General Comments

This area, as in 1964, was still under the influence of silt laden water (Chart 1). There was no apparent reduction in the fish population in 1964, but the recent count indicated a sharp drop. This apparent drop may be biased considering the very high degree of turbidity during the observation period. The vasiform *Acropora* that remain in this area were often heavily invested with necrotic areas.

Most of the reef had a covering of blue-green algae and 0.5 to 1 mm of silt.

On days of maximum precipitation a 1.5 m deep freshwater lens covered the inner bay reefs, and the absence of winds prevented mixing of water masses. Sedentary or weakly motile organisms which could not avoid the fresh water were exterminated in great numbers. Hydrogen sulfide arising by decompositional processes aided in the depletion of oxygen, and extensive inner bay reef communities were decimated (Fig. 50). In this reef kill the areas of greatest dieoff occurred toward the southern end of the bay which normally receives the highest freshwater inputs as well as municipal sewage inputs (Gundersen and Stroup, 1967). Measurements made three years after the catastrophe by DiSalvo (unpublished data) indicated increased N and terrestrial sediment content in dead coral formations nearer to shore, and a greater depletion of oxygen within spaces of nearshore dead coral formations.

Another reef catastrophe caused by freshwater inflow was reported by Goreau (1964) for a Jamaican reef. A 17-inch rain occurred over a three day period on the fringe of hurricane Flora (1963) resulting in the widespread death of and physiological stress to corals which were subjected to salinities as low as 7 ^{o}/oo.

The major indicator of physiological stress was the "bleaching" of coral colonies; that is, loss of their symbiotic zooxanthellae. As established by Yonge (1931), shading of hermatypic corals causes the zooxanthellae to be lost. This "bleaching" indicator is also prime evidence for man-induced disturbance on otherwise undisturbed coral reefs. Although the oil spill at Guanica, Puerto Rico has not been studied from the particular point of view of coral reef disturbance, Diaz-Pifferer (1962) has mentioned that corals in the area of the oil spill showed the bleached appearance.

Many corals along the south coast of Puerto Rico west of Ponce are becoming white where petrochemical wastes are being released from industrial complexes. From del Valle, (1968); Cerame Vivas, et al. (1968); Austin and Austin (1968), and Ramos, (1968) there are suggestions that industrial wastes on the south shores of Puerto Rico near Guayanilla and Tallaboa bays are receiving enough wastes to change turbidity and affect reefs. Bleached corals are numerous and there are suggestions that blue-green algae are increasing their coral boring activities as a result of the stresses. A grave threat to the reefs on the southern shores of Puerto Rico are the turbidity stresses induced by uncontrolled waste discharges upstream.

Restricted Circulation

DiSalvo (unpublished data) has observed that when parts of the coral reef frame (dead coral head community) are removed from high wave energy zones and maintained under reduced conditions of water circulation, an internal anaerobiosis develops which causes the death of the internal aerobic community. Man-induced disturbances to reefs are also cited in the chapter on sugar mill wastes - which mentions the effects of these wastes on Hawaiian reefs. Mats of bagasse fiber accumulating on the reef surface reduced circulation and depleted oxygen, producing deteriorated conditions confirmed in the laboratory.

Stress of Biological Imbalance

Predatory decimation of stony corals has been reported since 1965 over many miles of Australia's Great Barrier Reef due to a population explosion of the poison spined starfish Acanthaster planci (Harding,1968). Chesher (1969 Science 165:280-283) reported extensive damage to the reefs of Guam,with reef kill (90%) as rapid as 1 km / month over 38 km of fringing reef . The starfish feed on coral polyps, leaving behind the bare skeleton. The dead coral surfaces are then invaded by an atypical algal community which aids in causing degradative effects on the reef framework. Normally occurring fishes leave the affected areas, seriously lowering the catches of reef fish by islanders. In a 1969 survey report for the U.S. Dept. of the Interior (through Westinghouse Research Labs, Pittsburgh,Pa.), Chesher indicated that numerous reefs of well known Pacific islands were being attacked (Saipan,Tinian,Truk,Ponape,Palau, Majuro, and Arno). Although the starfish increase may be related to dredging,blasting,predator removal by shell collectors, and pollutional influences such as insecticides, the true cause-effect relationship remains obscure.

Conservation

Practical and esthetic grounds encourage efforts for the conservation of coral reef areas, especially for recreation and study. Important advances have been made by the conservation of St.John and Buck Island in the Virgin Islands. A great deal of fishing is usually done near coral reefs. Coral reefs are optimally designed natural breakwaters which influence the development and control of tropical coastlines.Part of this development includes the production and retention of calcareous sands which form tropical beaches, a major basis for tourism in Hawaii, Florida, Puerto Rico, and the Virgin Islands. Interference with normal reef growth and metabolism may alter sand formation and retention and allow erosion and disappearance of the beaches.

Chapter B-3

TROPICAL MARINE MEADOWS

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Tropical meadows are beds of underwater grassy vegetation found in shallow, clear tropical waters. The principal rooted plants in U. S. systems are broad-bladed turtle grass Thalassia testudinum; narrow bladed Diplanthera wrightii (Halodule); cylindrical manatee grass, Syringodium filiforme (Cymodocea); branching Ruppia maritima; leafy Halophila; and interdispersed bottom clumps of algae. The blades support small epiphytic organisms. On the bottom among the blades of vegetation are many tropical animals of great diversity and beauty including urchins, sea cucumbers, tube worms, molluscs, and fishes, many of which burrow into holes in the bottom. The vegetation forms a heavy layer of matted stems that makes a firm carpet with the sediments, much of which consists of the skeletal fragments of the animals. Many of the animals live by eating the bottom material, extracting organic food from it and releasing the mineral matter which is often limestone white. The food chain starts with the photosynthesis of the bottom plant beds, followed by microbial decomposition in the old grass blades, consumption of the partially decomposed fragments by the bottom organisms, and their consumption in turn by the larger fishes. Many of the bottom animals are filter feeders that keep the waters clear while also processing the remains from the decomposition. Bacteria are abundant, partly decomposing the grass material into a soup which is then consumed by the bottom fauna.

Distribution

Tropical meadows occur in waters of moderate current energy 2 to 25 feet in depth in Puerto Rico, the Florida Keys, and South Texas. In zones of high wave energy, especially at the surface where waves break, the meadows are displaced by coral and algal reef systems. In deeper and more quiet waters, the meadows apparently displace the coral system, being better adapted to use somewhat lesser light intensities and currents.

The tropical meadow resembles somewhat the temperate vegetation meadows covered in Chapter C-7A by Phillips, except that there are fewer stresses and less seasonal change . The populations adapt to a relatively minor pattern of seasonal change in insolation, temperature, and economy of food flows. Diversities and specialization are better developed towards complex organization of ecological communities, less energy being involved in seasonal adaptations.

Some members of the tropical meadows are found in subtropical zones such as North Florida (Strawn, 1961) and South Texas, but the general pattern of complexity, variety, and white calcareous sediment tends to disappear outside of the tropical uniformity of climate. The turtle grass system in Texas is an example of the northern limit of the tropical meadow where many temperate properties of seasonal pulse, variation, and change are imposed on species associations, which fluctuate less in more southern distributions.

EXAMPLES

High Diversity Meadows in Puerto Rico

Turtle grass beds floor the shallow waters among patch reefs near La Parguera, Puerto Rico (see Fig. 2 in Chap. B-4). Studies at the University of Puerto Rico are cited in Figs. 1-4 and Tables 1-7. In Fig. 1 Glynn (1964) diagrams the scatter of larger animals in heavy beds that occur in several feet of clear, high salinity water. With very even temperature regimes, these beds at 18 degrees N. Latitude receive only about 25% insolation differences with season. Burkholder, Burkholder, and Rivero (1959) provide tables 1 and 2 on the weight of the beds (from 2.4 to 32.9 tons per acre, the rhizomes underground increasing in coarse sand). Gilberto Cintrón in an unpublished report found 3.2 tons/acre in Fajardo in eastern Puerto Rico. Chemical analyses showed balanced concentrations of many amino acids, 25% ash, and 13% protein. Around, on, and within the blades, large concentrations of bacteria were counted (Table 5). Margalef (1962) found the photosynthetic pigments most abundant some distance behind the tip of the Thalassia blade (Fig. 3). The tip is the oldest part and the ratio of chlorophyll a to other pigments absorbing in the violet was greatest with age, the tips becoming coated with attached and diversified algal epiphytes. Margalef uses the ratio as a measure of complexity. Chlorophyll also was large in some of the many algae dispersed among the blades (Table 7). The high productivity of the whole bed is shown in Fig. 2 where the oxygen curves of water drifting over turtle grass are used to calculate gross photosynthesis (10.5-14 g/m^2/day in February). Odum, McConnell and Abbott (1958) found 0.43 g/m^2 chlorophyll a in these beds, a moderately high quantity. The various indices show productive utilization of the light and a complex community of animals and bacteria. Table 8 from Warmke and Almodovar (1963) shows small molluscs associated with particular algal species in small proportions, not overgrazing, suggesting programmatic organization of roles. Another example of specific control is the antibiotic activity of the calcareous green alga Halimeda (Fig. 4).

Meadows in the Bahamas

Stable environments producing tropical meadows with high diversity also occur beyond the Gulf stream over shallows of the Bahama banks as shown by Kornicker (1958) in Bimini sound (Fig. 5). Note the many species of associated algae and animals. The broad Bahama banks are largely covered with bottom meadows, sometimes thin and sometimes thick in shallow waters. The cumulative actions of photosynthesis in the shallow waters lower the calcium and carbonates in the water (Fig. 6 and 7) because of the calcareous precipitation, mainly by organisms. The ratio of these elements to chloride decreases over the banks.

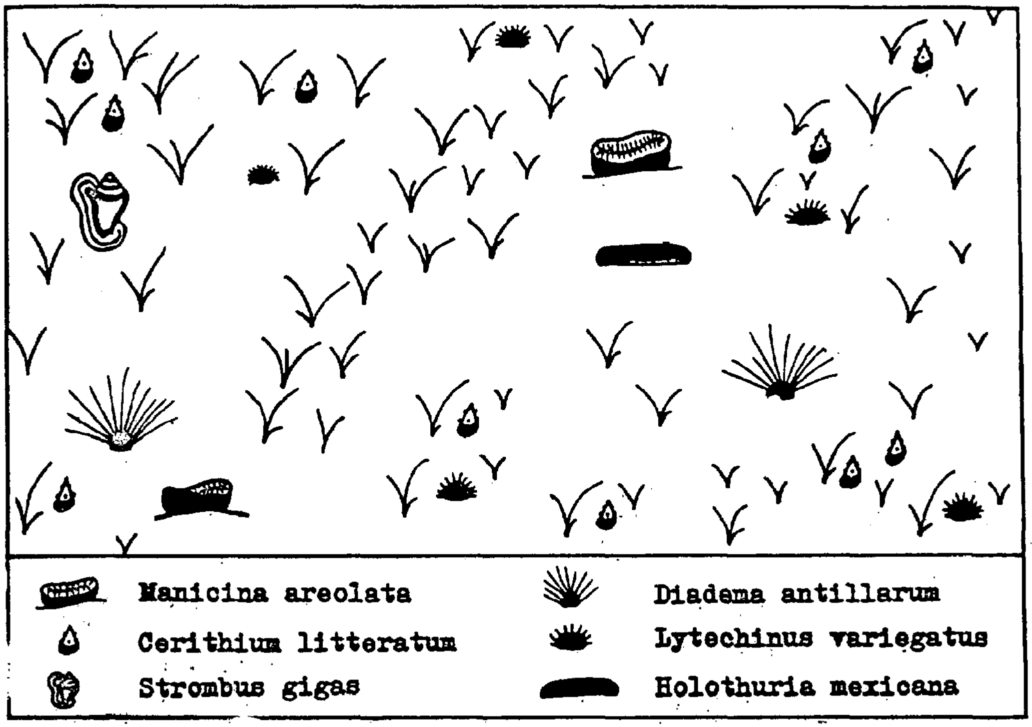

Manicina areolata
Cerithium litteratum
Strombus gigas
Diadema antillarum
Lytechinus variegatus
Holothuria mexicana

Fig. 1. Components of turtle grass in southwestern Puerto Rico from Glynn (1964).

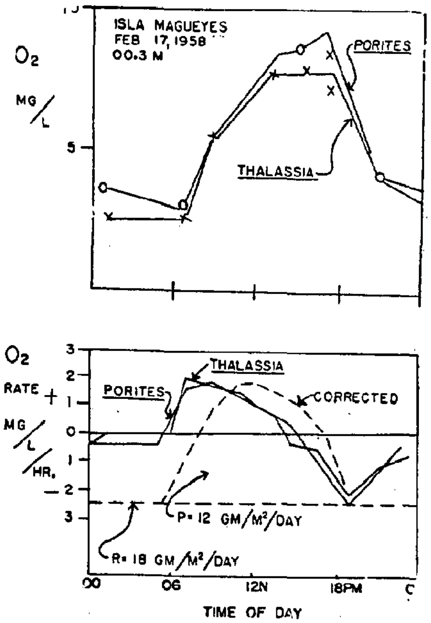
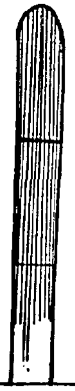
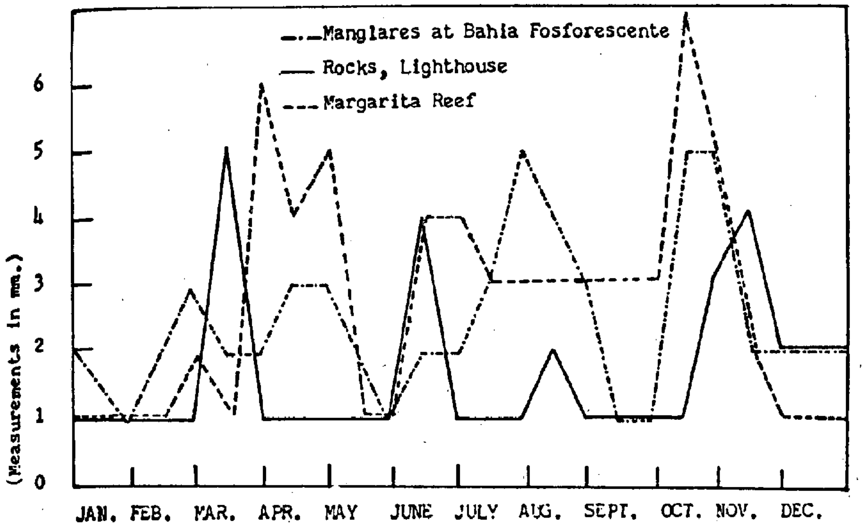


Fig. 2. Oxygen productivity data comparing coral reef and turtle grass in Puerto Rico (Odum, Burkholder, and Rivero, 1957).

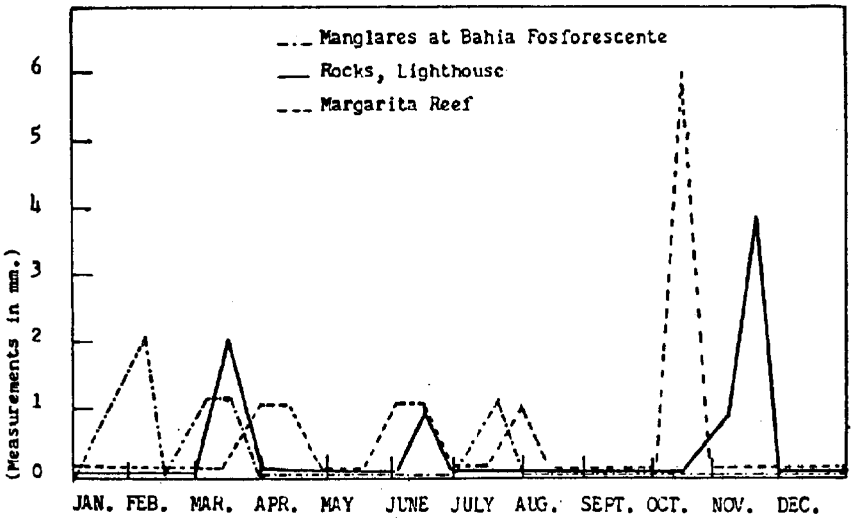


Tanto por mil de clorofila a	Relación D_{430}/D_{665}
1,45	2,42
2,38	2,26
0,72	2,11

Fig. 3. Chlorophyll and pigment absorption ratios of a Thalassia blade in Puerto Rico (Margalef, 1962).



The antibiotic activity of *Halimeda opuntia* on *Staphylococcu aureus* in one year with readings taken on the 1 and 15 of each month.



The antibiotic activity of *Halimeda opuntia* on *Escherichia coli* in one year with readings taken on the 1 and 15 of each month.

Fig. 4. Antibiotic activity of a calcareous green alga on bacteria (Almodovar, 1964a).

Tables 1-5. Stocks and chemical contents of turtle grass in southwestern Puerto Rico (Burkholder, Burkholder, and Rivero, 1959).

ABLE 1. *Standing crops of whole* Thalassia *plants (leaves, rhizomes, roots) in per acre.*

Location	Tons per acre
West Las Palmas	16.1–21.9
East Las Palmas	12.1–18.3
East of La Parguera	2.4– 3.1
Bahia Fosforescente	3.7– 4.9
La Cueva, West	5.8–25.7
La Cueva, North	17.6–32.9

TABLE 2. *Influence of bottom sediments upon the ratio of roots and rhizomes to* ves *in* Thalassia.

Location	Dry weight in grams		
	Roots and rhizomes (RR)	Leaves (L)	$\frac{RR}{L}$
Fine mud East of La Parguera	38.5	12.8	3.0
Mud and sand West Las Palmas	378.5	79.7	4.7
Coarse sand East Las Palmas	336.5	46.3	7.3

TABLE 3. *Proximate analysis of* Thalassia *leaves,* Porites, *phytoplankton,* Spartina *leaves and Coastal Bermuda grass leaves. All data are given in per cent dry weight, except the caloric values.*

Determinations	*Materials*				
	Thalassia leaves	*Porites* coral	Plankton L.I.S.	*Spartina* leaves	Bermuda grass
Protein (N × 6.25)	13.1	3.4	14.6	9.8	13.1
Fat	0.5	1.4	3.7	2.4	2.0
Ash	24.8	90.4	59.5	11.5	4.6
Crude fibre	16.4	1.5	1.6	31.0	33.0
Other carbohydrate	35	1.9	15.6	45.3	47.3
Calories/100 grams	19[illegible]	23	154	375	....

TABLE 4. *Amino acid constituents of the leaves of* Thalassia testudinum *expressed in per cent (gm. amino acid per 100 gm. of dried material). For comparison, typic data obtained for leaves of* Spartina alterniflora *are also given.*

Amino acids	*Thalassia* % of dry matter	*Spartina* % of dry matter
Arginine	0.702	0.182
Aspartic acid	1.120	no assay
Glutamic acid	1.090	no assay
Histidine	0.310	0.028
Isoleucine	0.249	0.143
Leucine	0.693	0.214
Lysine	0.720	0.769
Methionine	0.187	0.038
Phenylalanine	0.465	0.128
Threonine	0.204	0.256
Tryptophan	0.049	0.086
Valine	0.317	0.149

TABLE 5. *Quantitative estimates of the aerobic bacteria present in t*... *environmen of* Thalassia *at Magueyes Island, Puerto Rico.*

Source of Samples	*Bacteria per gm. of Sam*
1. Surface water outside *Thalassia*	627
2. Surface water above *Thalassia*	600
3. Water in bed of *Thalassia*	3,968
4. Water from agitated *Thalassia*	192,000
5. Mud from bed of *Thalassia*	3,700,000
6. *Thalassia* ground in mortar	15,104,000

Table 6. Trace elements in turtle grass in Puerto Rico (Stevenson and Ufret, 1966).

Levels of Fe, Mn, and Ni in thalli and stems of P. gymnospora *collected at Punta Higuero and* T. testudinum *collected at La Parguera, Puerto Rico* (*μg/g dry wt*)

	Fe		**Mn**		**Ni**	
	P. gymnospora	*T. testudinum*	*P. gymnospora*	*T. testudinum*	*P. gymnospora*	*T. testudinum*
	5,700	210	150	44	28	17
	4,700	310	85	36	23	19
	4,100	290	84	53	32	23
	5,600	270	120	54	28	22
	4,000	93	80	72	27	19
	4,400	450	89	47	24	24
	520	140	91	36	26	15
$\bar{X}$	4,100	250	99	49	27	20
s_x	1,733	120	25	12	3	3

Table 7. Chlorophyll and pigment ratios in green and brown algae in Puerto Rico (Margalef, 1962).

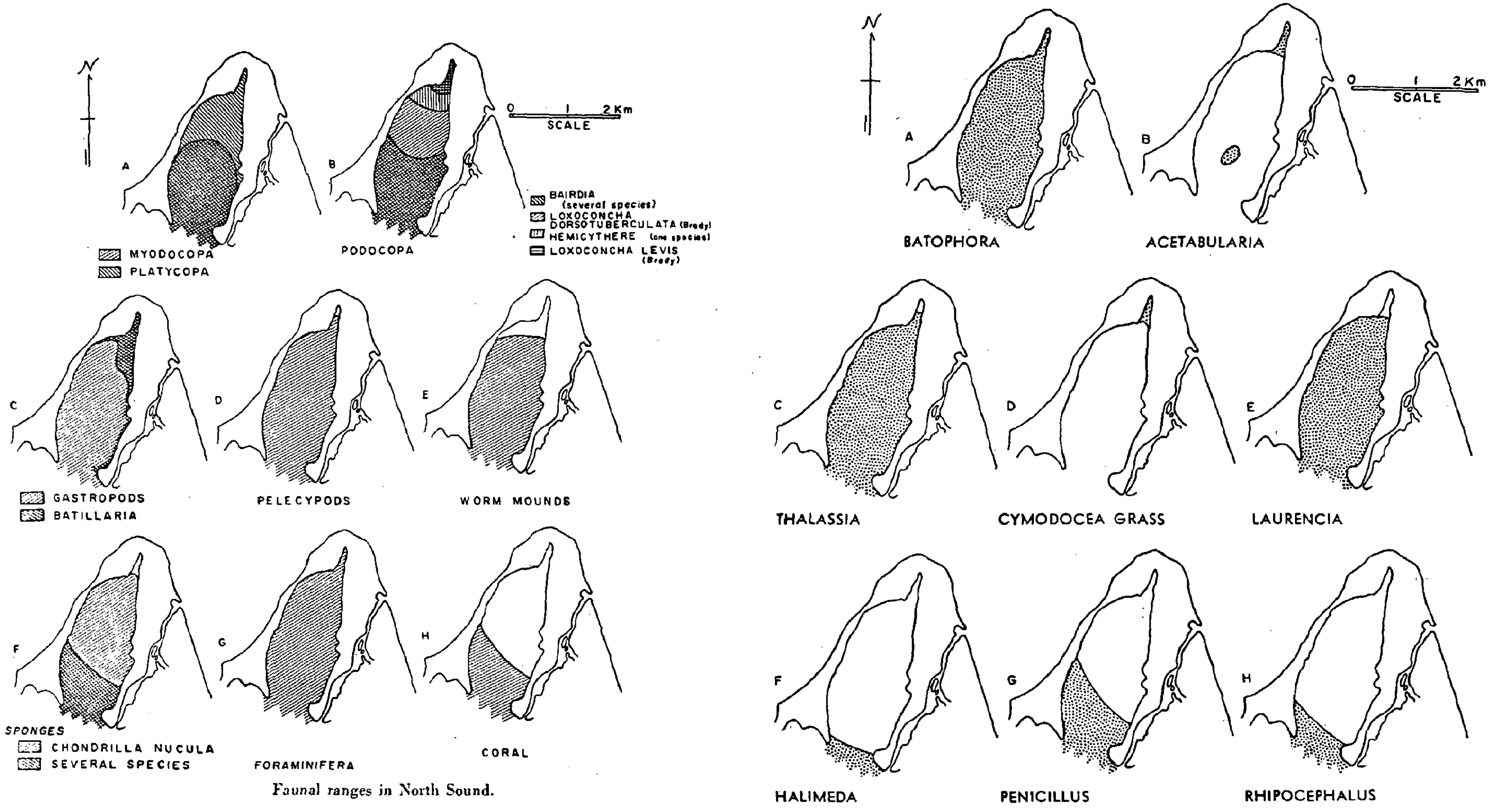
Especie	Tanto por mil de clorofila a	D430/D665
Penicillus capitatus (clorofícea)	1,8	1,69
Halimeda opuntia (clorofícea)	0,27*	1,81
Dictyota cervicornis (feofícea)	1.	2,52

*Referido a peso seco total, Halimeda contiene mucha caliza.

Table 8. Associations of small mollusca with algae in Puerto Rico (Warmke and Almodovar, 1963).

Distribution of Pelecypods and Amphineura on 10 Species of Green Algae[14]

PELECYPOD SPECIES	**SPECIES OF ALGAE**										
	Bryopsis pennata (4 lots)	*Caulerpa crassifolia* (2 lots)	*Caulerpa racemosa* (11 lots)	*Caulerpa sertularioides* (2 lots)	*Cladophoropsis membranacea* (6 lots)	*Halimeda opuntia* (13 lots)	*Halimeda tridens* (1 lot)	*Penicillus capitatus* (3 lots)	*Rhizoclonium hookeri* (5 lots)	*Udotea flabellum* (3 lots)	**Average per lot on all Green Algae (50 lots)**
Brachidontes exustus	1.5		0.5		1.2	0.5	1.0				0.5
Condylocardia smithii			0.4		0.2	0.1		1.0			0.2
Arca imbricata						0.2					0.1
Musculus lateralis						0.1				0.3	0.1
Arca zebra						0.1					0.02
Barbatia cancellata			0.1								0.02
Gouldia cerina						0.1					0.02
Lima sp.						0.1					0.02
Misc. young	0.3		0.2		0.2	0.2	1.0				0.2
Total Pelecypods	1.8		1.1		1.5	1.3	2.0	1.0		0.3	1.02

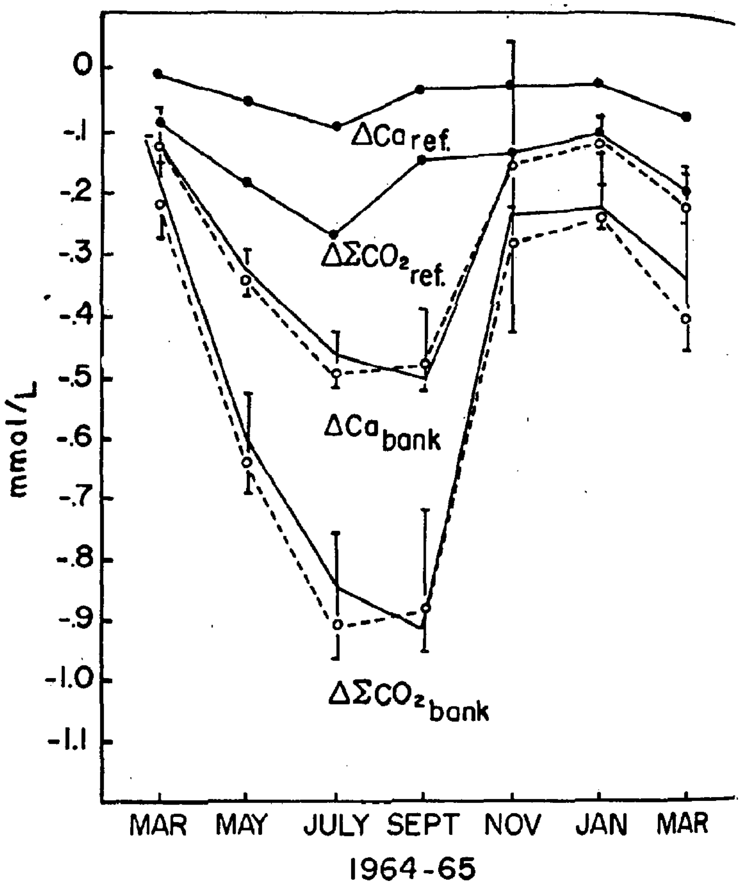


Faunal ranges in North Sound.

Floral ranges in North Sound.

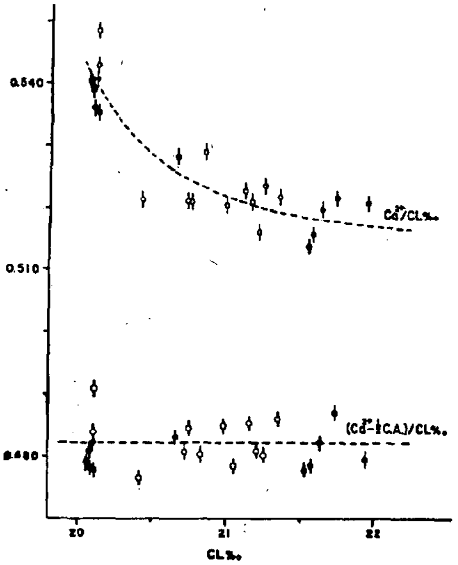
N
0 1 2 Km
SCALE
A
MYODOCOPA
PLATYCOPA
B
PODOCOPA
BAIRDIA (several species)
LOXOCONCHA DORSOTUBERCULATA (Brady)
HEMICYTHERE (one species)
LOXOCONCHA LEVIS (Brady)
C
GASTROPODS
BATILLARIA
D
PELECYPODS
E
WORM MOUNDS
F
SPONGES
CHONDRILLA NUCULA
SEVERAL SPECIES
G
FORAMINIFERA
H
CORAL
N
A
BATOPHORA
B
ACETABULARIA
0 1 2 Km
SCALE
C
THALASSIA
D
CYMODOCEA GRASS
E
LAURENCIA
F
HALIMEDA
G
PENICILLUS
H
RHIPOCEPHALUS

Fig. 5. Bottom organisms in Bimini sound, British Bahamas (Kornicker, 1958).



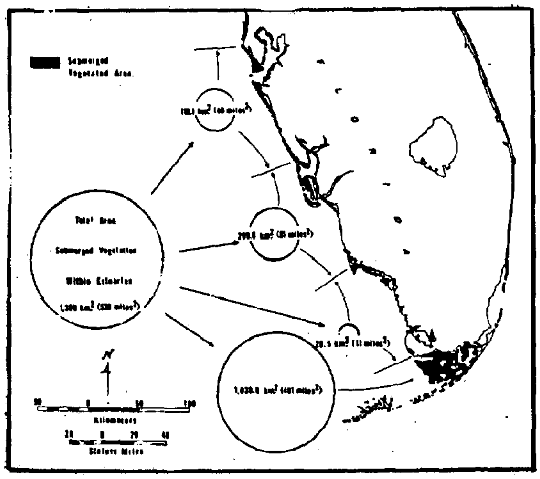
Seasonal ΣCO_2 and calcium losses on the Great Bahama B The solid dots are the average for surface and bottom (7m) values from a hour bank edge reference (25°15'N, 79°10'W). The open dots are the av for surface values from a 25-hour drift station on the bank (24°57'N, 7 W). The dashed line is the average for near bottom (5m) values from drift station. Vertical lines show diurnal range.

Fig. 6. Loss of carbonates and calcium from Bahama banks with turtle grass (Traganza 1967).



Calcium : chlorinity and "noncarbonate" calcium : chlorinity ratios on the Great Bahama Bank as functions of chlorinity. Solid circles are values obtained from samples collected in July 1964. Solid circles are values obtained from samples collected in July 1964. Open circles are for September 1964. Ratios are in units of mmol liter^{-1} : g kg^{-1}. Chlorinity is in units of g/kg.

Fig. 7. Loss of calcium relative to chlorida accompanying photosynthetic and thermal stimulation of calcification in tropical banks with turtle grass (Traganza and Szabo, 1967).


Submerged Vegetated Area.
Total Area
Submerged Vegetation
Within Estuaries
N
Kilometers
Statute Miles

Areas of submerged vegetation in Florida estuaries from Tampa Bay to the Florida Keys.

Fig. 8. Bottom marine meadows of south Florida (McNulty, 1968).

Meadows of South Florida

Especially at the tip of south Florida in Florida Bay, turtle grass meadows are a principal vegetation type (Fig. 8). Extensively studied, their communities are diverse as suggested by species lists (Tables 9-14).

Patterns of turtle grass distribution with depth on a shoal are mapped by Kissling (1965) in Fig. 9, Thalassia being found in waters deeper than 1 or 2 feet. Phillips (1960) reported similar zonation of Thalassia with depth (Fig. 10), other vegetation such as shoal grass (Diplanthera) growing in shallows. Another example of Thalassia distribution is shown in Fig. 11 from Lynts (1966b). Humm (1964) found 113 species of epiphytic algae on turtle grass under stable high salinity conditions. Patterns of bacterial distribution in turtle grass are suggested in Table 14. Meyers (1968) found large diversity in fungi and reported that some characteristic species such as Lindra thalassiae are important in decomposition and mineralization of the old Thalassia blades (Tables 13 and 15; Fig12).

Studies of animals in undisturbed beds show very high diversities especially in Thalassia (Tables 9-12). Hopper and Meyers (1967b) from beds near Key Biscayne found nematodes important in interactions with the fungi. High species diversity curves and population curves with summer maxima, are given in Fig. 13. Sea urchins such as the poison spined Diadema (Fig. 14) were common. Randall, Schroeder, and Starck (1964) found $1.2/m^2$ in grass flats. Although the bottom communities predominate there is a plankton component moving up from the bottom during the night and among the blades (Fig. 15). Data on the stable hydrographic climate are given in Fig. 16 and Table 16 (covering long-term salinity).

A study of the dominant turtle grass (Thalassia testudinum) in benthic meadows at Miami was made by Jones (1968). By measuring oxygen release in enclosures placed over the plants, food contributions were measured through a year and extrapolations were made to the natural community from data on standing crop of biomass. Some of Jones' results are given in Figs.16-19 showing relatively moderate changes during the year at Miami. Winter insolation, however, was almost half that in April and May, and gross photosynthesis varied similarly. Respiratory contributions of the plants were about one to two tenths of the gross production. These results do not give the whole community production under normal mineral cycling circumstances, but they do suggest the similarities of the seasonal regime. Hurricanes produced large grass windrows, but turned out to be a minor action per area (Thomas, Moore, and Work , 1961).

Free water measurements of oxygen metabolism were made by Tabb, Dubrow and Manning (1962) in some inshore areas disturbed by salinity fluctuation and by Jones (1963) in less disturbed waters. Estimates of overall photosynthetic productivity and system respiration (Table 17) compare with Texas data (Table 18) but are less than results in stable salinity zones studied in Puerto Rico and one measurement at Long Key, Florida (Odum, 1957) in Fig. 20. Erratic salinities in southwest Florida waters (Fig. 21) contrast with more stable conditions near the Gulf Stream (Fig. 16).

Table 9. Invertebrate animals in Florida turtle grass (O'Gower and Wacasey, 1967).

DOMINANT SPECIES (IN ORDER OF DOMINANCE) IN *Diplanthera*, *Thalassia*, AND SAND BEDS, KEY BISCAYNE AND VIRGINIA KEY

Area	*Diplanthera*	*Thalassia*	Sand
Key Biscayne	*Onuphis magna* *Nothria stigmatis* *Clymenella mucosa* *Anachis avara* *Divaricella quadrisulcata* *Codakia orbicularis* *Chione cancellata*	*Loimia medusa* *Onuphis magna* *Codakia orbicularis* *Diopatra cuprea* *Chione cancellata* *Euclymene coronata* *Alpheus normanni*	*Clymenella mucosa* *Divaricella quadrisulcata*
Virginia Key	*Phascolion* sp. "a" *Chione cancellata* *Anodontia alba*	*Codakia orbicularis* *Chione cancellata* *Semiodera roberti* *Amphioplus abditus* *Amphiodia pulchella* *Prunum apicinum* *Loimia medusa* *Panopeus occidentalis* *Notomastus luridus* *Terebellides stroemi*	*Batillaria minima*

Table 10. Diversities and other properties of grass beds in Florida (O'Gower and Wacasey, 1967).

DESCRIPTIVE INDICES FOR COMMUNITIES IN *Diplanthera* (D), *Thalassia* (T), AND SAND BEDS, KEY BISCAYNE AND VIRGINIA KEY

Indices	Key Biscayne			Virginia Key		
	D	T	S	D	T	S
[1]Fisher & Williams α	16.202	19.437	5.578	10.434	15.439	3.932
[2]Dahl s/α	0.946	0.607	0.599	1.135	0.641	0.609
[3]Authors Md./$\bar{x}$	0.264	0.413	0.214	0.108	0.740	0.023

[1] Index of diversity.
[2] Index of uniformity.
[3] Index of dominants.

Table 11. Fishes trawled in shallows in which bottom meadows are important (Roessler, 1965).

—The number of individuals per tow compared to the expected values of a negative binomial distribution for selected species

Species	Mean	Coefficient of contagion	Chi-square	d.f.
Area I, day				
Syngnathus floridae	0.80	457.49		
Monacanthus ciliatus	1.80	1,663.9		
Apogon alutus	0.25	1.2290	0.11	1
Haemulon plumieri	10.55	2.0322	6.61	7
Lachnolaimus maximus	0.80	0.7496	0.97	1
Sparisoma rubripinne	27.60	3.0782	6.20	6
Monacanthus hispidus	7.60	2.8899	7.89	7
Sphaeroides spengleri	0.45	0.8422	0.22	1
Diodon holacanthus	0.30	7.0069	0.06	1
Opsanus beta	0.20	464.93		
All species combined	52.00	3.4593	6.10	8
Area I, night				
Syngnathus floridae	0.95	433.45		
Apogon alutus	1.20	1.6674	2.84	2
Haemulon plumieri	18.50	1.8670	7.74	8
Lachnolaimus maximus	0.85	1.7292	0.39	2
Sparisoma rubripinne	12.70	1.5564	5.47	5
Monacanthus ciliatus	0.70	1,173.7		
Monacanthus hispidus	5.35	3.5439	2.34	7
Opsanus beta	1.15	402.23		
All species combined	44.30	2.6202	3.12	7
Area II, day				
Syngnathus floridae	1.05	3.3716	1.40	1
Haemulon plumieri	1.30	1.2385	1.42	2
Calamus arctifrons	0.50	948.78		
Lagodon rhomboides	0.30	7.0069	0.06	1
Sparisoma rubripinne	3.00	1.5343	2.71	5
Monacanthus ciliatus	2.00	1.0559	4.02	3
Monacanthus hispidus	5.15	0.6137	5.44	4
Sphaeroides spengleri	0.70	1.9823	1.35	1
All species combined	15.80	1.3119	5.78	7
Area II, night				
Syngnathus floridae	1.60	228.38		
Apogon alutus	0.30	7.0069	0.06	1
Haemulon plumieri	2.90	0.9448	4.47	4
Calamus arctifrons	0.60	9.3125	0.19	1
Lagodon rhomboides	1.25	3.3244	2.87	2
Sparisoma rubripinne	2.10	3.0965	4.23	4
Monacanthus ciliatus	1.70	4.5853	2.45	3
Monacanthus hispidus	7.60	4.2174	18.34	8
Lactophrys quadricornis	0.45	2.4288	0.50	1
Opsanus beta	0.70	483.82		
Sphaeroides spengleri	0.45	2.4288	0.50	1
All species combined	23.20	15.441	4.49	3
Area III, day				
Haemulon plumieri	0.05	431.87[1]		
Sparisoma rubripinne	0.40	1,369.8		
Monacanthus ciliatus	0.10	448.85		
Monacanthus hispidus	0.25	471.50		
All species combined	1.15	0.9871	2.76	2
Area III, night				
Eucinostomus argenteus	0.95	0.6957	0.73	1
Haemulon plumieri	0.55	920.99		
Sparisoma rubripinne	0.45	939.95		
Microgobius microlepis	0.45	434.24		
Monacanthus ciliatus	0.25	747.39		
Monacanthus hispidus	0.40	869.46		
All species combined	4.50	1.1921	4.09	4

[1] Example of a single individual in all 20 samples—approaches the Poisson distribution.

Index diversity (α) based on Fisher's logarithmic distribution for trawl samples collected in Biscayne Bay and comparison with observed data

Area	Number of individuals	Number of species	Index of diversity	Standard error	Chi-square	d.f.
Day						
I	1,052	31	6.003	1.0780	17.288**	4
II	316	26	6.813	1.3325	3.759	4
III	23	8	4.328	1.6100	1.668	2
Night						
I	1,886	35	6.934	1.1955	15.933**	5
II	464	38	9.699	1.5840	7.458	7
III	90	21	8.679	1.9251	5.327	4

** Significant at the 99% level.

Table 12. Some mollusca with bottom vegetation in Florida (Moore, 1963).

Gastropods	Number per square meter
Bittium varium	2170
Rissoina chesneli	5440
Caecum pulchellum	13220
Mitrella lunata	130
Pelecypods	
Brachidontes exustus	7940
Amygdalum papyria	230

Table 13. Trawl catch in shallows off south Florida (Moore, Jutare, Jones, McPherson, and Roper (1963).

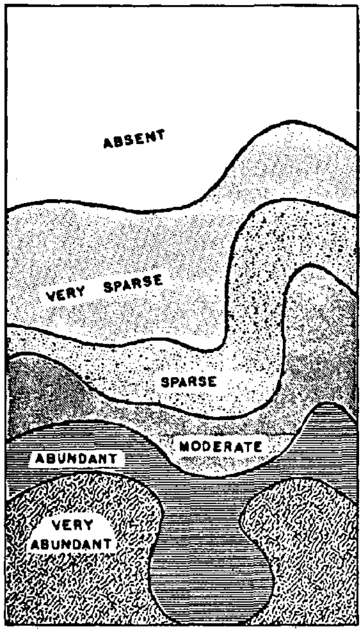
Numbers of shrimp and fish captured in trawl samples from Joe Kemp Channel and Sandy Key Basin in Florida Bay, April, 1959, a period when salinity values were near that of normal seawater in both areas.

Species	Joe Kemp Channel Catch from 5 trawl hauls. Bottom salinity 36.5 ppt	Sandy Key Basin Catch from 4 trawl hauls. Bottom salinity 37.2 ppt
Crustaceans		
Periclimenes longicaudatus	36	25
Tozeuma carolinensis	20	22
Hippolyte pleauracantha	7	129
Leander paulensis	7	10
Thor floridanus	5	12
Latreutes fucorum	4	8
Fish		
Lagodon rhomboides	28	115
Gerres cinereus	11	3
Lutjanus synagris	9	6
Bairdiella chrysura	2	14
Orthopristis chrysopterus	3	11

Table 14. Bacterial distributions in turtle grass of Florida (Wood, 1965).

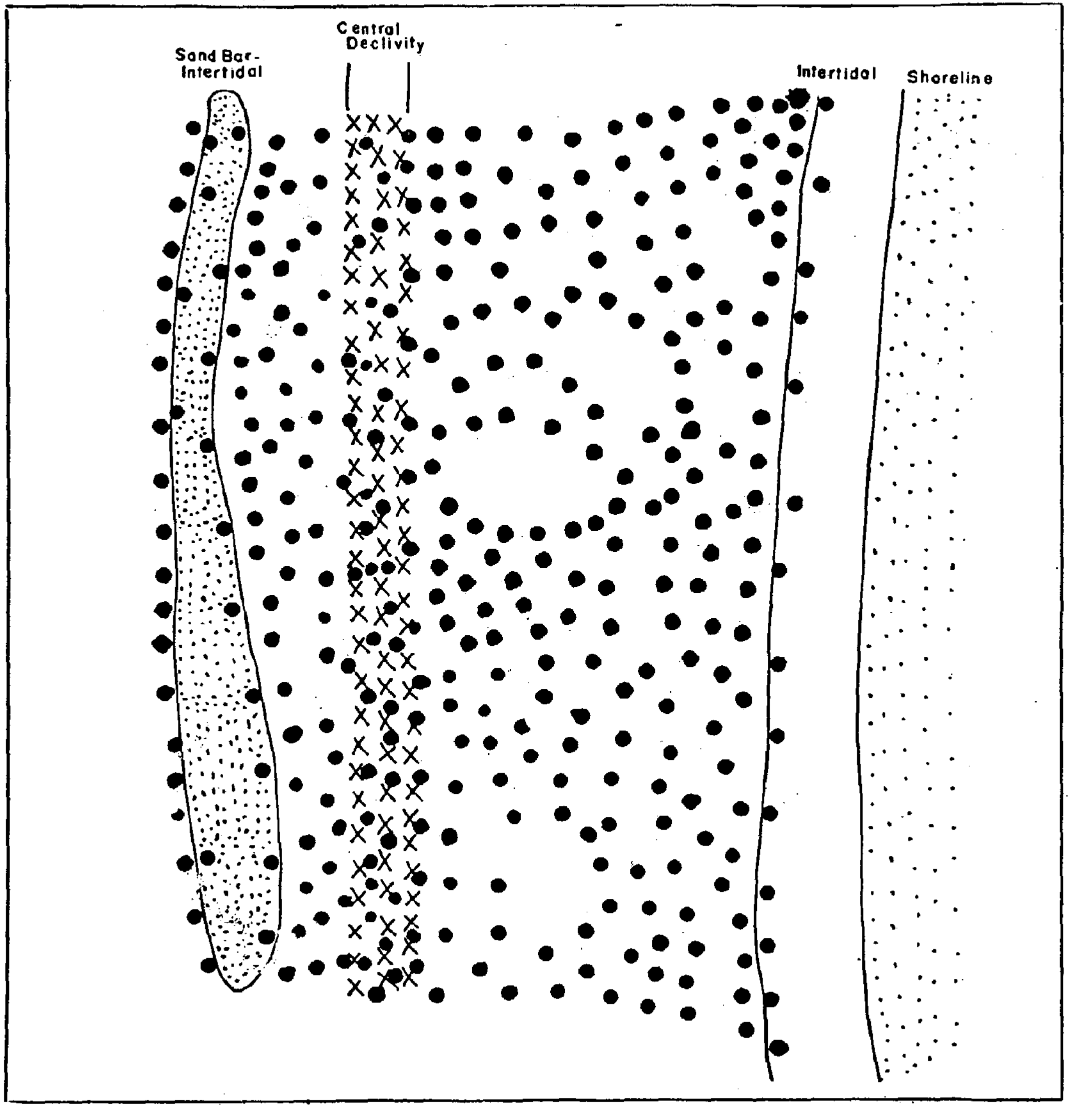
Occurrence of bacteria in various estuarine environments (percentage of species)

		Water		Sea-grass community
Species	Bottom	1 m from bottom	Surface	
Bacillus subtilis	45	39·5	22	10–25
B. megaterium	18	7	5·5	0
B. sphaericus	0	7·5	0	0
Corynebacterium globiforme	0	7·0	0	0
C. flavum	0	0	0	10
C. miltinum	0	0	0	5
Actinomyces spp.	18	0	5·5	10–25
Staphylococcus candidus	0	8	8	0
S. roseus	0	8	0	0
Mycoplana dimorpha	19	23	54	40
M. citrea	0	0	0	5
Sarcina lutea	0	0	5·5	0
Pigmented strains	20	38	27·5	50
Ratio gram pos./gram neg. strains	1·9	2·0	0·7	0·9


ABSENT
VERY SPARSE
SPARSE
MODERATE
ABUNDANT
VERY ABUNDANT

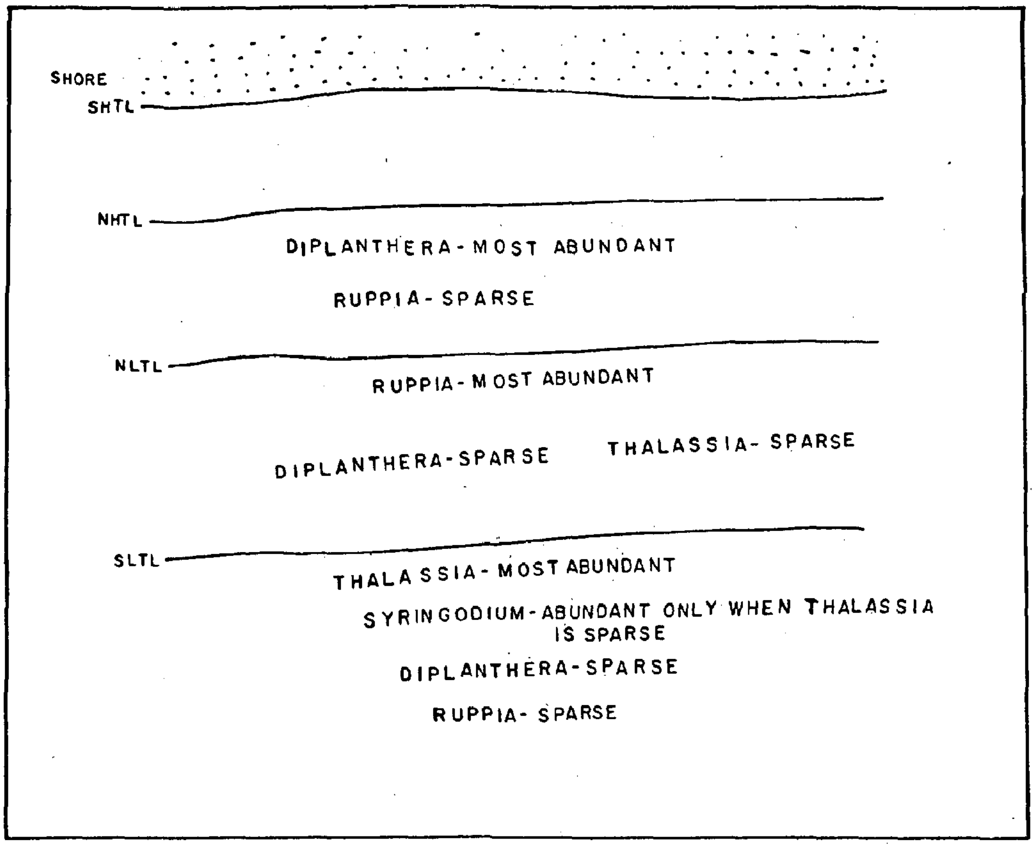
Relative distribution of *Thalassia testudinum.*

Fig. 9. Zonation of turtle grass diminishing as water shoals (Kissling, 1965).


Sand Bar-Intertidal
Central Declivity
Intertidal
Shoreline

Schematic drawing of Beach Drive station showing intertidal zones and maximum depth declivity with location of grasses. These symbols are used: ● -*Diplanthera (Ruppia* in late winter and spring); X -*Thalassia* and *Syringodium.*

Fig. 10A. Zonation of bottom spermatophyte plants by depth in Tampa Bay, Florida, (Phillips, 1960a).

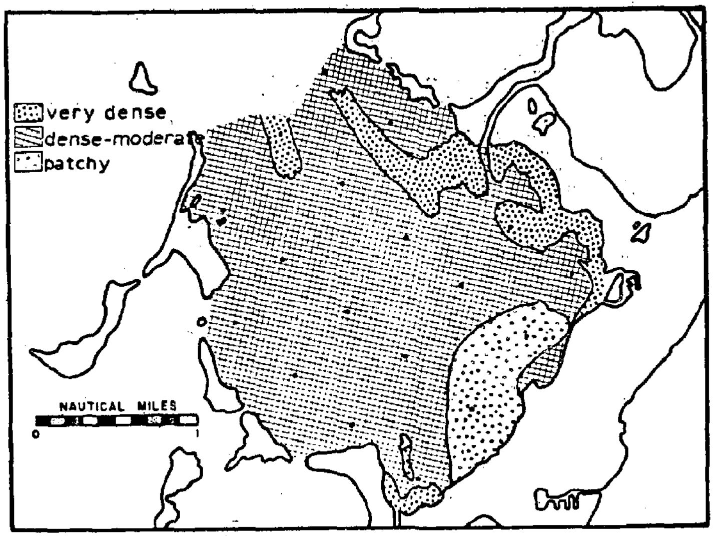

SHORE
SHTL
NHTL
DIPLANTHERA-MOST ABUNDANT
RUPPIA-SPARSE
NLTL
RUPPIA-MOST ABUNDANT
DIPLANTHERA-SPARSE
THALASSIA-SPARSE
SLTL
THALASSIA-MOST ABUNDANT
SYRINGODIUM-ABUNDANT ONLY WHEN THALASSIA IS SPARSE
DIPLANTHERA-SPARSE
RUPPIA-SPARSE

Schematic drawing of seagrass zonation in shallow water. Valid only in areas with salinity over 25.0 o/oo.

Abbreviations are:

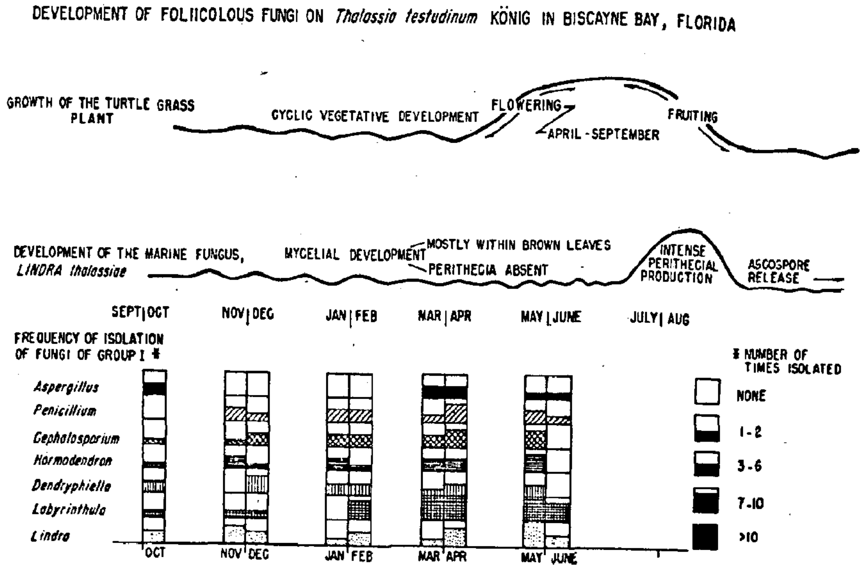
SLTL — slack low tide line	NHTL — neap high tide line
SHTL — spring high tide line	NLTL — neap low tide line

Fig. 10B. Summary diagram of bottom plants relative to depth in Florida (Phillips, 1960a).


very dense
dense-moderate
patchy
NAUTICAL MILES
0
1

Distribution of marine grasses (*Thalassia testudinum* König), showing intensity of growth, in Buttonwood Sound.

Fig. 11. Turtle grass bed among cays of south Florida (Lynts, 1966b).



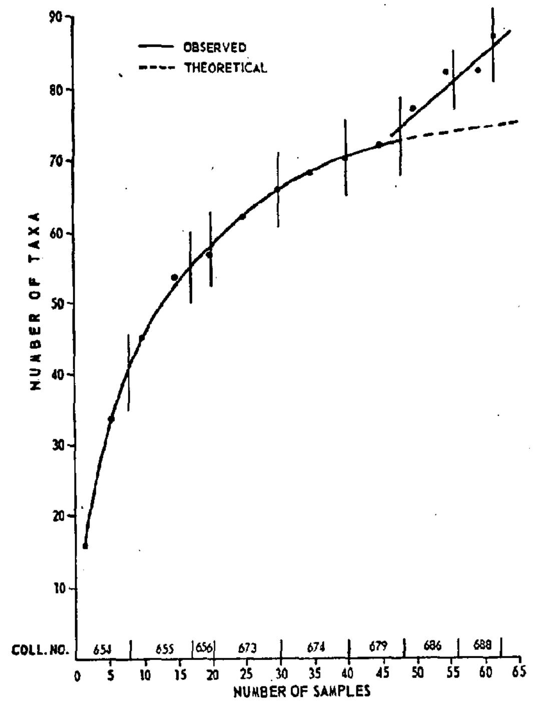
Schematic showing typical development of foliicolous fungi on turtle grass in Biscayne Bay, Florida.

Fig. 12. **Seasonal pattern of fungi in turtle grass beds of south Florida (Meyers 1968).**

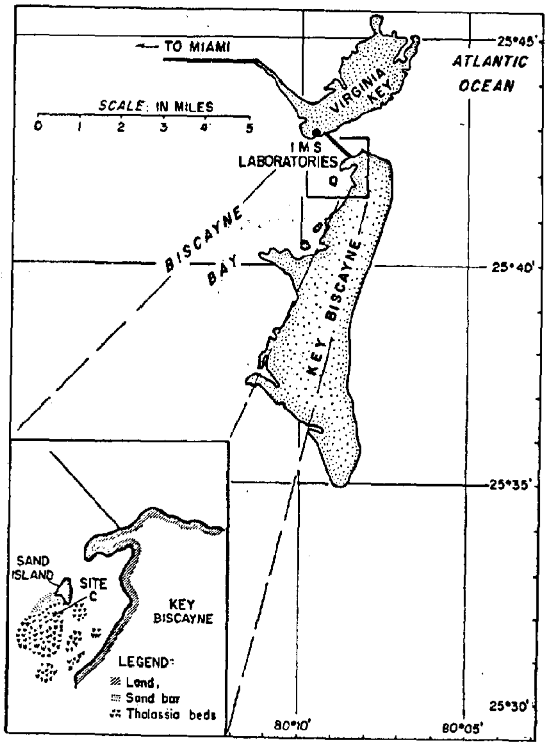
Table 15. Fungi in turtle grass (Meyers, 1968).

Fungi Present in Washed *Thalassia* Leaves

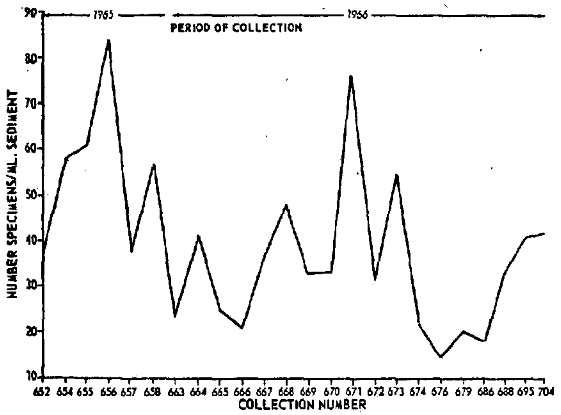
Group I Abundant, multi-isolations. Dominant mycota	Group II Scattered occurrence, 2-8 isolations	Goup III Uncommon, only single isolations	
Aspergillus	*Alternaria*	*Acrotheca*	*Monocillium*
Cephalosporium	*Aureobasidium pullulans*	*Botrytis cinerea*	*Nigrospora spherica*
Dendryphiella arenaria	*Ceratocystis* or *Cylindrocephalum*	*Fusidium*	*Phialophora*
Hormodendron	*Culcitalna*	*Geotrichium*	*Phomopsis*
Labyrinthula	*Cylindrocarpon*	*Gonabotryum fuscum*	*Spicaria violacea*
Lindra thalassiae	*Fusarium*	*Humicola*	*Torula*
Penicillium	*Phoma*	*Lulworthia*	*Zygosporium masonii*
Unidentified non sporulating mycelia	*Sporotrichium*	*Monilia*	Unidentified Ascomycete
	Varicosporina ramulosa		
	Unidentified pycnidial forms		
	Unidentified sporulating mycelia		



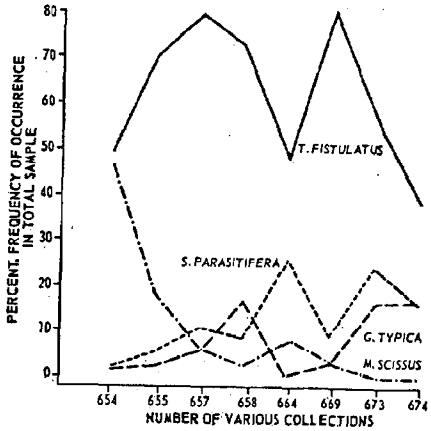
Relationship of number of taxa found to number of samples examined


TO MIAMI
25°45'
ATLANTIC
OCEAN
VIRGINIA KEY
SCALE: IN MILES
0
1
2
3
4
5
IMS
LABORATORIES
BISCAYNE BAY
25°40'
KEY BISCAYNE
25°35'
SAND
ISLAND
SITE
C
KEY
BISCAYNE
LEGEND:
Land,
Sand bar
Thalassia beds
80°10'
80°05'
25°30'

Location of collection site (Site C) in Biscayne Bay (Miami) Florida

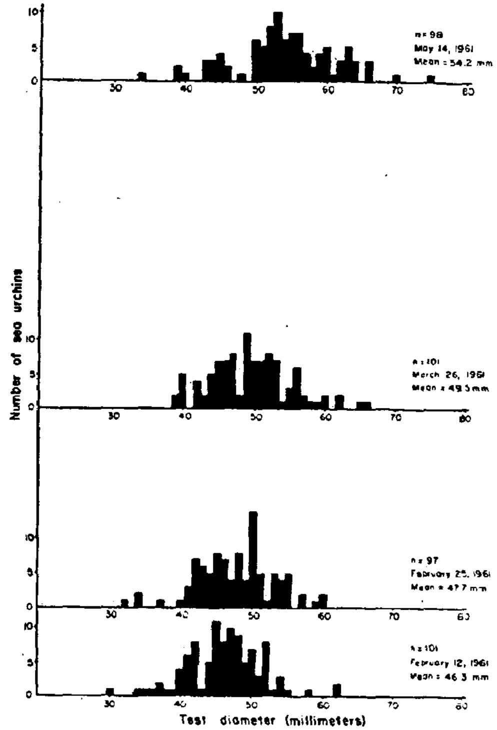


Population density or number of specimens over the entire collection period



Percentage frequency of occurrence of four species at position A_2

Fig. 13. Species diversities of nematodes in turtle grass beds of south Florida (Hopper and Meyers, 1967b).



Length frequency distributions of the test diameters of *Diadema antillarum* in four collections from a shallow *Thalassia* flat in Lignum Vitae Channel, Florida Keys. Distance between the abscissas of the four plots proportional to the time intervals between collections.

Fig. 14. Size of poison spine urchins in turtle grass beds of south Florida (Randall, Schroeder, and Starck, 1964).

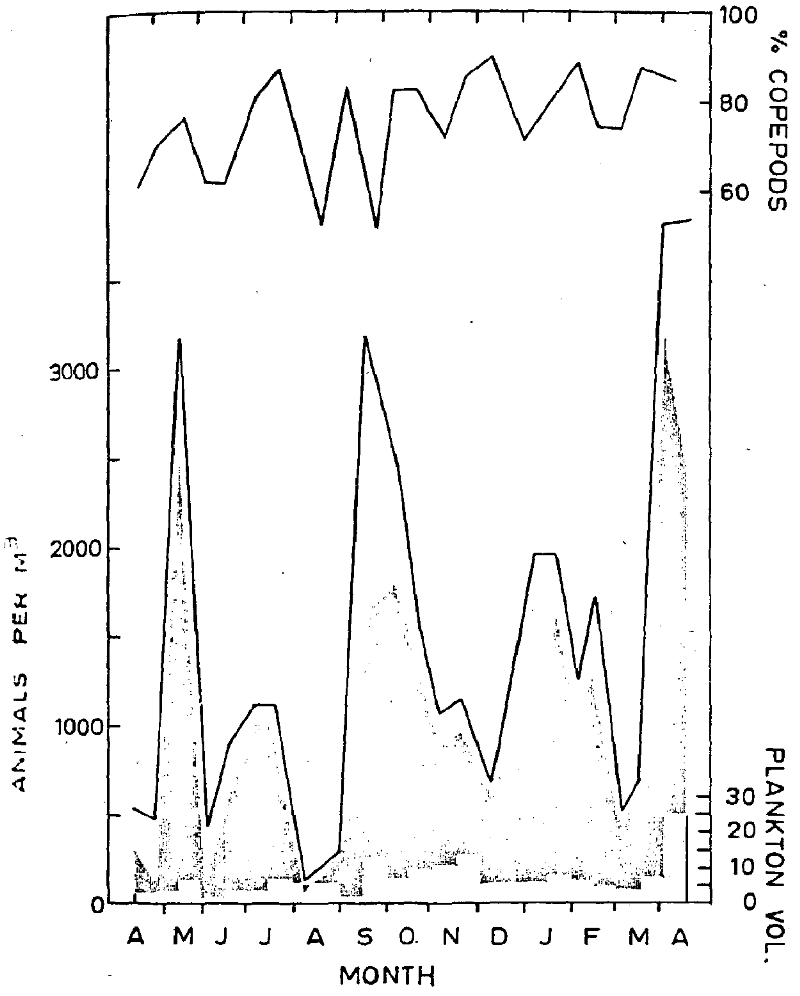


Fig. 15. Zooplankton among the Florida Keys (Woodmansee, 1958).

Table 16. Characteristics of bays of south Florida (Tabb, Dubrow, and Manning, 1962).

Long-term salinity characteristics of 10 stations along the salinity gradient during the period August, 1957, through May, 1962.

Station No.	No. monthly observations	Bottom salinity in ppt Lowest	Highest	Average	Long-term salinity as percentage seawater
Florida Bay 10	44	28.4	47.0	35.5	100.0%
Coot Bay 2	55	14.4	41.1	26.6	76.0%
Coot Bay 3c	65	8.0	41.1	25.3	72.2%
Coot Bay 5e	65	5.9	41.0	22.1	63.1%
Whitewater Bay I	55	4.0	40.0	18.7	53.4%
Whitewater Bay V	54	0.0	37.3	15.4	44.0%
Whitewater Bay VII	52	2.2	38.7	17.9	51.1%
North River VIIa	31	0.0	36.7	13.2	37.7%
East River	45	0.0	38.0	11.7	32.1%
Whitewater Bay XII	47	12.0	37.6	28.1	80.2%

Table 17. Productivity and respiration by the diurnal curve method in shallow bays of south Florida (Tabb, Dubrow, and Manning, 1962).

Results of metabolism studies at three stations.

Station	Date	P	R	K	Temp. range in C°	Salin. range in ppt.	P/R
Coot Bay							
3c	July '58	7.50	14.10	1.59	29.8-31.8	13.2-14.7	.531
3c	Oct. '58	1.10	4.97	.96	23.0-26.5	15.6-18.1	.221
3c	Jan. '59	1.50	1.30	.18	16.0-19.0	18.9-23.0	1.150
3c	Apr. '59	2.44	4.68	.89	24.0-27.0	26.7-27.7	.521
Whitewater Bay VII	Apr. '59	8.22	7.03	.85	24.0-27.0	25.1-26.4	1.110
Coot Bay 5e	Jan. '59	.81	1.66	.44	15.0-18.0	18.1-20.5	.490

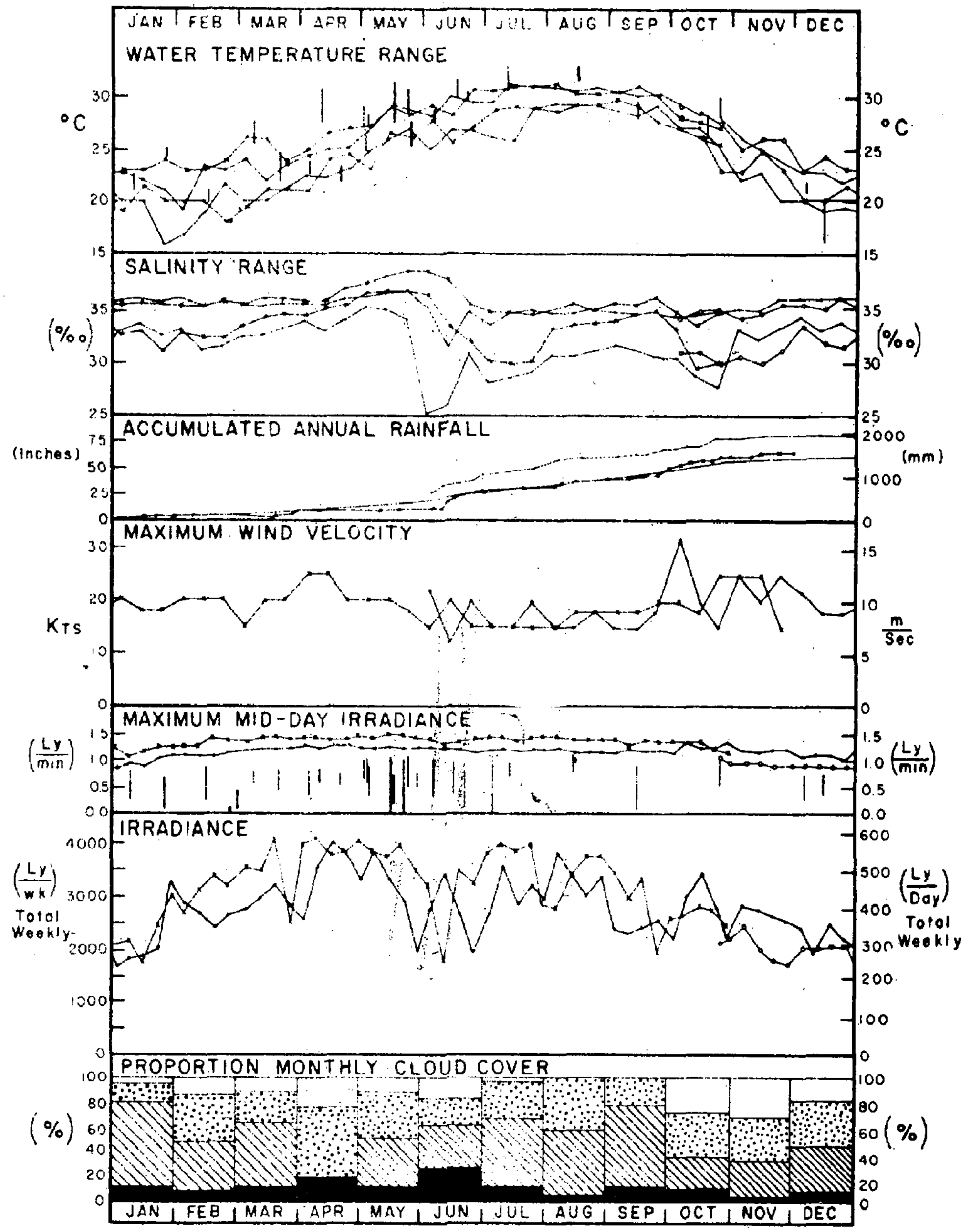
(P)—Photosynthesis; gm $O2/M^2$/day
(R)—Respiration; gm $O2/M^2$/day
(K)—Diffusion constant; gm $O2/M^2$/hour

Table 18. Comparisons of Florida and Texas by Tabb, Dubrow, and Manning (1962).

Tabb, *et al.*, (1959), and Tabb and Dubrow, (1962), contain the raw data from several 24 hour observations, not summarized here.

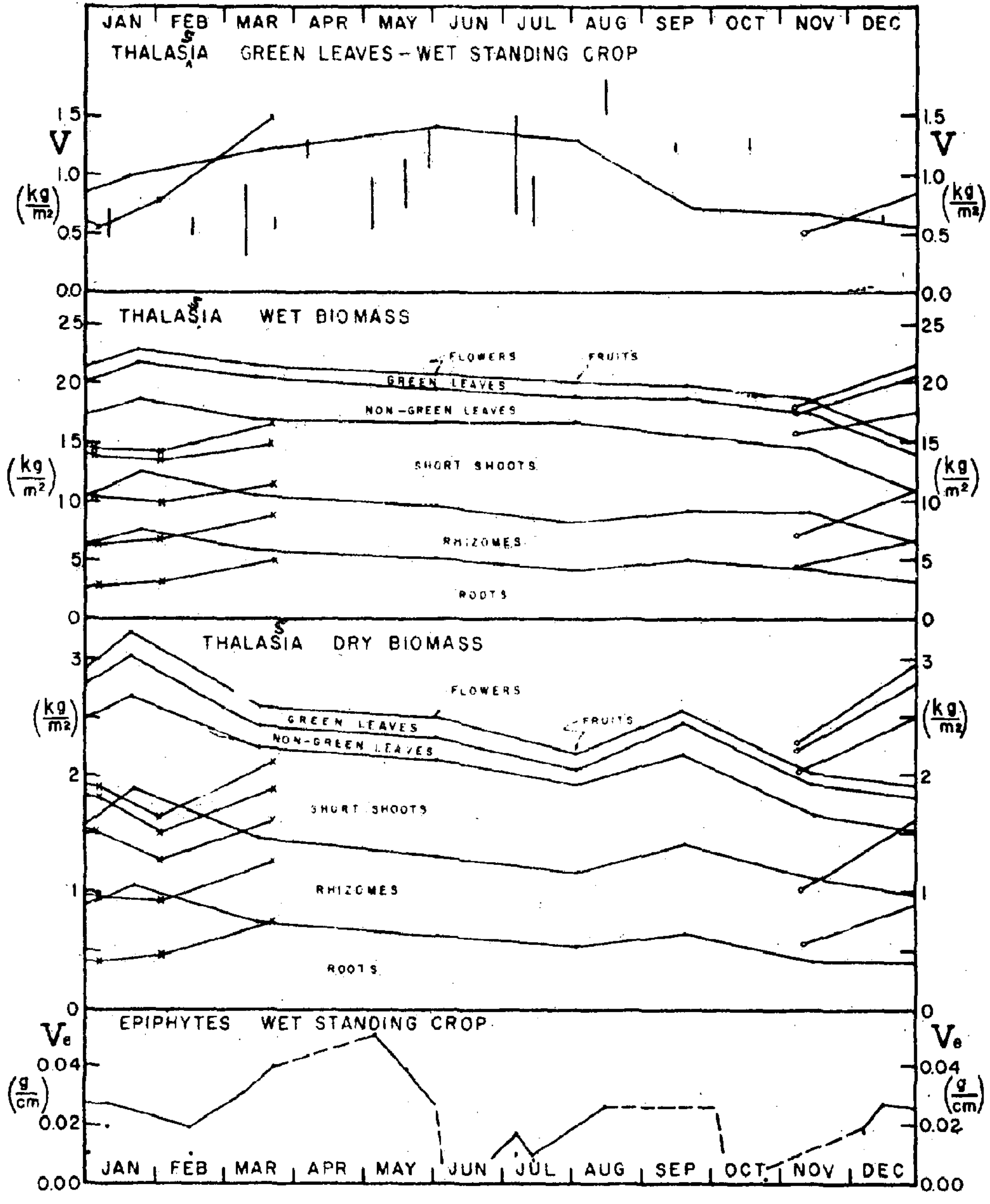
Results of free water diurnal curve studies in shallow Texas bays having conditions similar to those in Coot and Whitewater Bays. (Reproduced in part from Odum and Hoskin, 1958.)

Systems with both plankton and bottom mud components	P	R	K	P/R
(Similar to Coot Bay)				
Cedar Bayou, July 22, 1957; salinity 24.6; 1.5 M deep	5.6	17.6	1.5	.318
Mesquite Bay, July 22, 1957; salinity 15.5; algal bottom, 1.2 M deep.	3.8	7.3	1.2	.520
Copano Bay, Aug. 18, 1957; salinity 11.8	2.1	6.2	0.7	.339
Copano Bay, Oct. 20, 1957	1.6	1.65	—	.970
Aransas Bay, Rockport Pier, May 19, 1957, 1 M deep, salinity 21.0	6.3	4.8	0.6	1.340
Aransas Bay, Rockport Pier, Oct. 20, 1957, 1.3 M deep, salinity 18.7	6.1	7.8	1.8	.781
Systems with dominant bottom plant and animal communities; plankton unimportant.	**P**	**R**	**K**	**P/R**
(Similar to Whitewater Bay VII)				
Laguna Madre, Texas, Mean, *Diplanthera*-ooze 1957, annual curve.	4.3	5.6	0.2-1.4	.758
Redfish Bay, Port Aransas, Texas, *Thalassia* beds; Ransom Island, mean of 5 days in all seasons.	11.4	17.0	0.6-1.7	.670



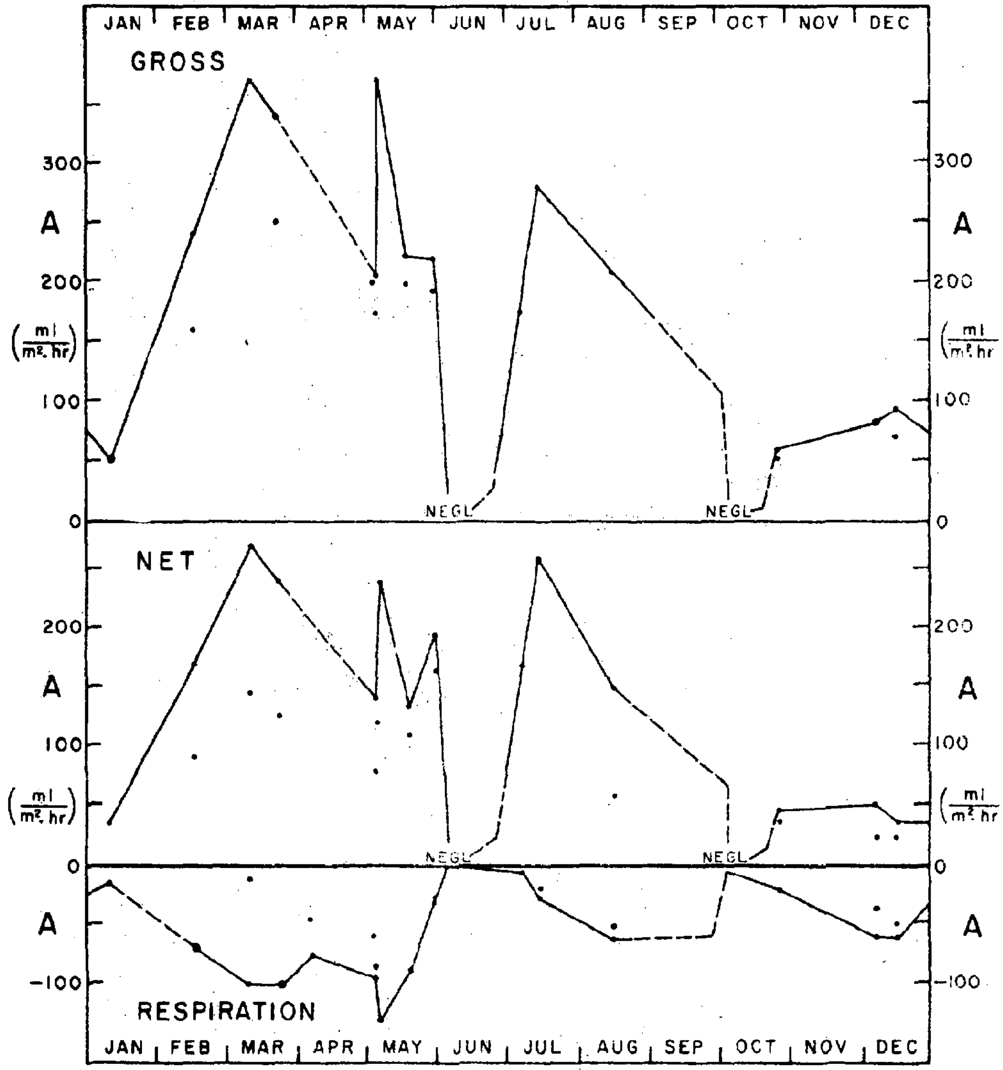
Environmental conditions in the vicinity of Virginia Key, Miami, for 1965 (o), 1966 (.), and 1967 (x). Water temperature and salinity range are from data taken in Bear Cut at the Institute of Marine Sciences. Accumulated rainfall and maximum wind velocity are from data provided for Miami by the U.S. Weather Bureau (ESSA) published in the Miami Herald. Irradiance and cloud cover data are recorded on an instrument at the Institute of Marine Sciences.

Fig. 16. Seasonal record of sun's energy and other properties of region of the marine meadows in south Florida (Jones, 1968).



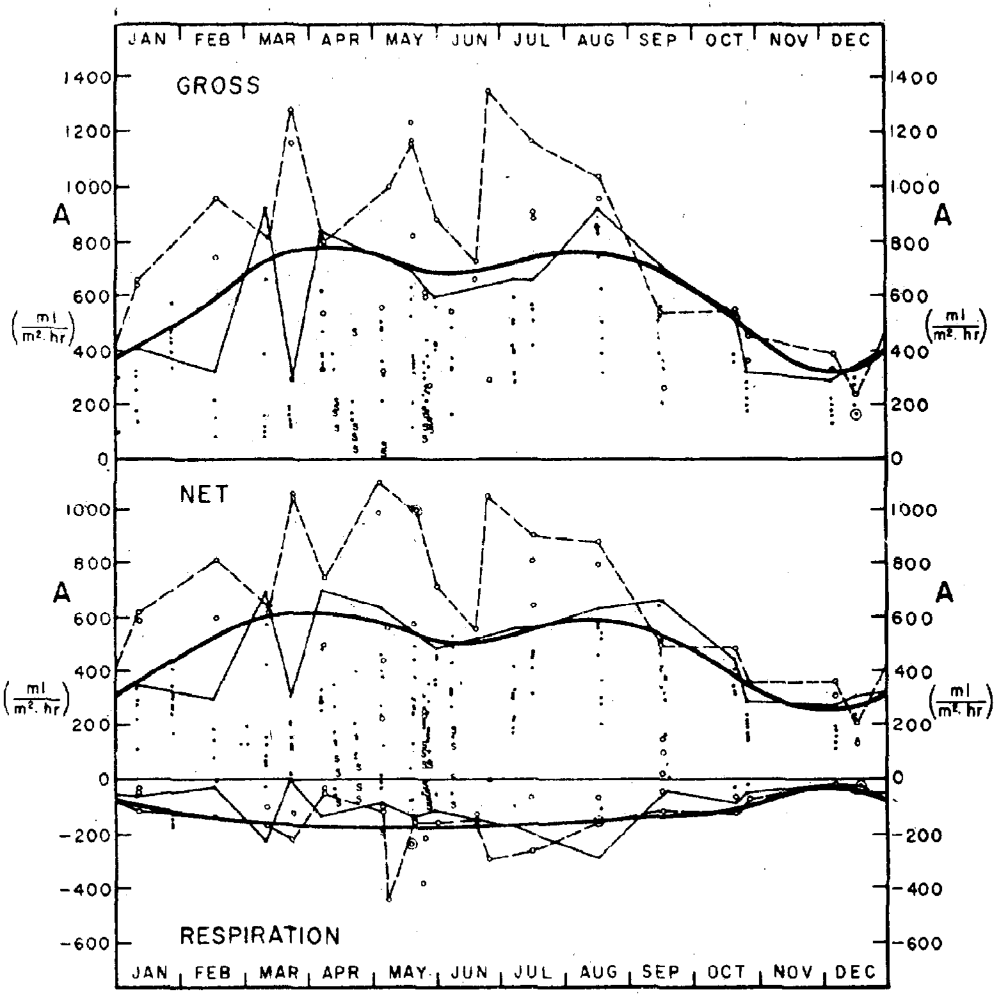
Seasonal variation in standing crop of green leaves and biomass of total plant material (wet and dry weights) for Thalassia and standing crop of the epiphytes. The data for Thalassia are based on one-tenth square meter samples at Bear Cut, Miami, with the vertical lines for standing crop representing ranges of observed occurrences from bell jar experiments. The data for the epiphytes, in grams per centimeter of Thalassia leaf blade, are weights obtained in connection with the manometer experiments.

Fig. 17. Mass of benthic plants in a south Florida turtle grass bed (Jones, 1968).



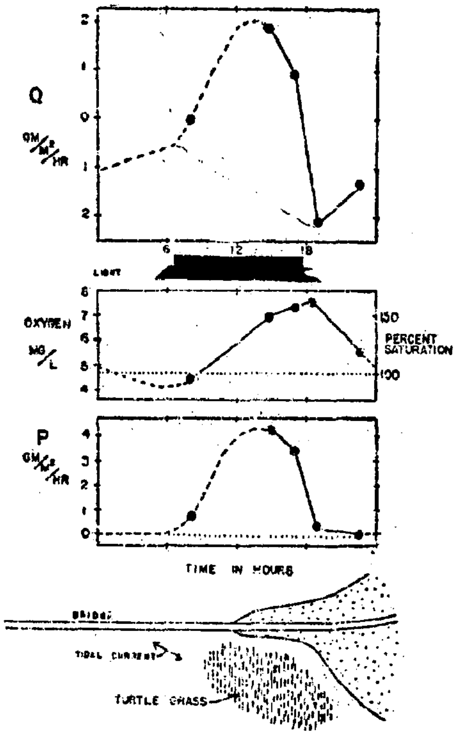
Seasonal variation in primary productivity per unit area (A) by the epiphytes of Thalassia. These data are derived from those in Figure 17 on the basis of several assumptions.

Fig. 18. Seasonal record of primary production and repsiration of turtle grass epiphytes in south Florida meadows (Jones, 1968).



Seasonal variation in primary productivity per unit area (A) by Thalassia. The heavy curves reflect the seasonal trends. Data from "bare sand" bottoms are represented by the letter "s." Other symbols are as in Figure 7.

Fig. 19. Seasonal record of productivities and respiration of isolated turtle grass plants in chambers (Jones, 1968).

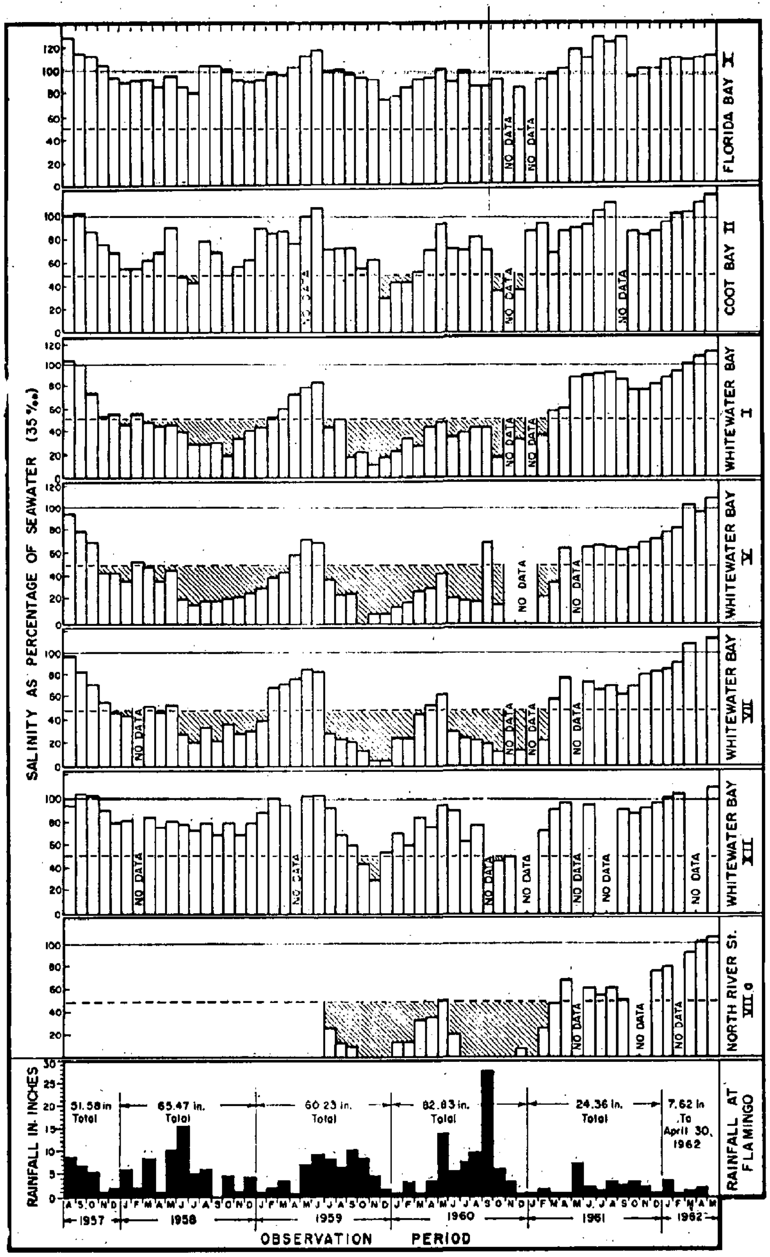


Rate of oxygen change (*Q*) and primary production (*P*) on an area basis in masses of water moving over beds of turtle grass along the causeway on Long Key, Florida, August 14, 1955. The oxygen curve (middle graph) is used to correct for diffusion loss during the day so as to derive the production curve (*P*) from the oxygen rate-of-change curve (*Q*). Parcels were followed with fluorescein dye by a wading observer. Points are the mean differences between duplicate samples (Table 3). Current velocity varied from 0 to 0.22 m/sec.

Oxygen changes (mg/L) near moving dye spots over Thallassia *grass flats Aug. 14, 1955, Long Key, Fla.*

Time of start	Time lapse in minutes	Depth m	Oxygen at start	Oxygen at end	Oxygen change	Rate of oxygen change gm/m²/hr
2:35 pm	7	0.9	6.85	7.05		
			6.81	7.10	0.24	1.86
3:56 pm	14	0.9	7.21	7.49		
			7.20	7.44	0.25	0.96
6:41 pm	5.5	0.9	7.79	7.80		
			8.04	7.62	−0.21	−2.1
10:24 pm	10.4	0.75	5.67	5.45		
			5.80	5.40	−0.32	−1.4
7:53 am	4.6	1.05	4.47	4.43		
			4.48	4.52	0	0

Fig. 20 Primary production measurement from oxygen changes in free water (Odum, 1957).



Monthly average salinity as percentage of seawater (35.0 ppt) at 7 representative stations along the salinity gradient and monthly rainfall at Cape Sable. Shaded portion indicates months when salinity fell below 17.5 ppt or 50 per cent of seawater.

Fig. 21. Erratic rainfall and salinities in estuarine waters of southern Florida (Tabb, Dubrow, and Manning, 1962).

Seasonal variations in growth rate and reproductive activity, possibly in phase with the pulse of photosynthesis of the community, are given in Figs. 22-23.

Principal swimming members of the tropical meadow include the commercial pink shrimp Penaeus duorarum. The grass beds serve as nurseries for the fast growth of these shrimp in Texas and Florida, correlated with spring energy pulse (Idyll, Tabb and Yokel, 1967) (Saloman, 1965). In Texas they migrate out the passes into the Gulf around the first of June. In Florida they migrate west, the larger shrimp being caught in the fishery near Dry Tortugas. The steady yields of the Tortugas pink shrimp fishery suggests a stable pattern of recruitment from the high diversity turtle grass nursery of Florida Bay (Fig. 24).

From free water changes in oxygen Jones (1963) estimated dry matter production in waters including some turtle grass and some patch reefs to be 0.8-2.0 $g/m^2/day$.

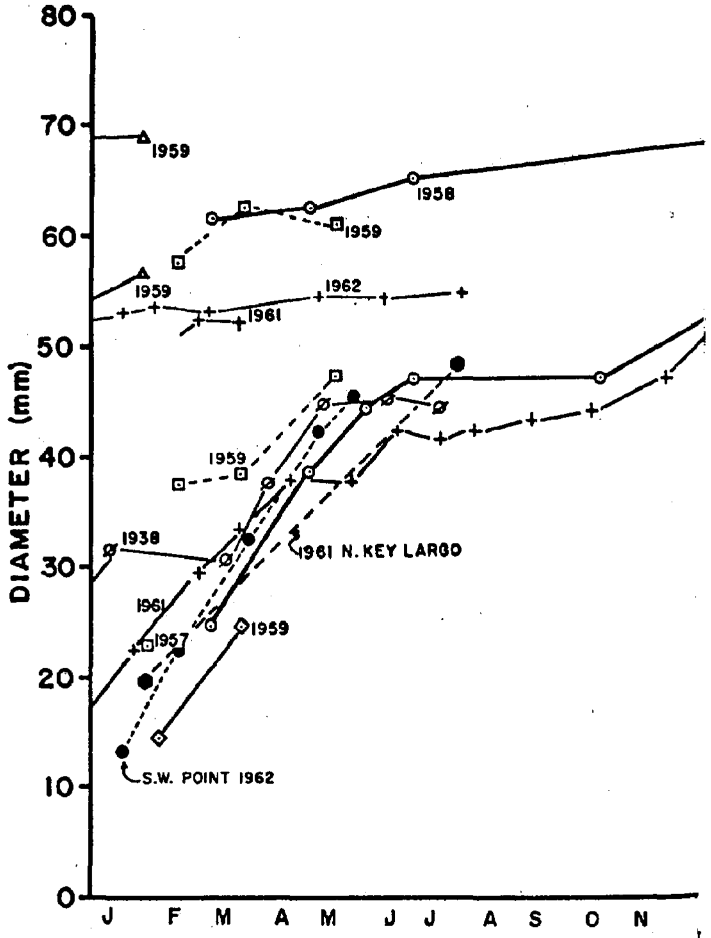
Turtle Grass at Redfish Bay Texas

A case history on which several investigators have made studies over a several year period is Redfish Bay, Texas (Fig. 25). Some principal data are assembled as Tables 19-21 and Fig. 25. In Fig. 26-27 are studies on sediment and ostracods by Grossman (1965) and Kornicker (1964b). Bacteria were studied by Volkman and Oppenheimer (1960, Fig. 28). Larger animals were collected in drop nets by Hoese and Jones (1963, Fig. 29 and 30). Trace elements (Tables 19-21) and amino acids in waters amidst the grass are given by Park (1963, Fig. 31). Total gross photosynthesis and system respiration were determined by freewater measurements of oxygen and carbon-dioxide (Odum and Hoskin, 1957; Odum and Wilson, 1962). Fig. 32A shows 24 hour records of oxygen and productivity. Fig. 32B shows records in a large enclosure set down over the grass. Fig. 33 (Odum, 1968) summarizes the data on productivity and sums other seasonal records in these grass beds. Fig. 34 shows results of Parker (1966) with radioactive tracer uptake experiments using 4 elements. Fig. 35 (Odum, 1963a) has simplified diagrams of carbon and zinc cycles in turtle grass. See Conover (1964) and Kornicker (1970) for additional details.

DISCUSSION

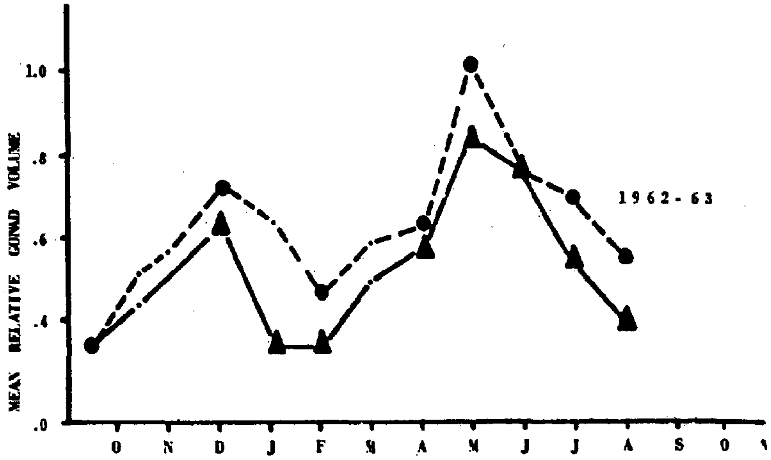
Salinity Adaptations

The plant members of the diverse tropical high salinity meadows have varying tolerances and abilities to succeed in lower and more variable salinity conditions. In system conditions which are classified as other system types McMillan and Moseley (1967) report salinity tolerances for 4 species (Fig. 36). Meyers (1968), studying salinity adaptation of fungi, found species important to the high stable salinity Thalassia beds not as well adapted to low salinities as some other forms (Fig. 37). In general the species with least tolerance predominate in the high salinity situations where the salinity adaptability has little use and presumably is an energy drain. In Texas Ruppia takes over when there are surges of low salinity water and Diplanthera when hypersaline regimes develop. In Fig. 38 and 39 Hammer (1968)



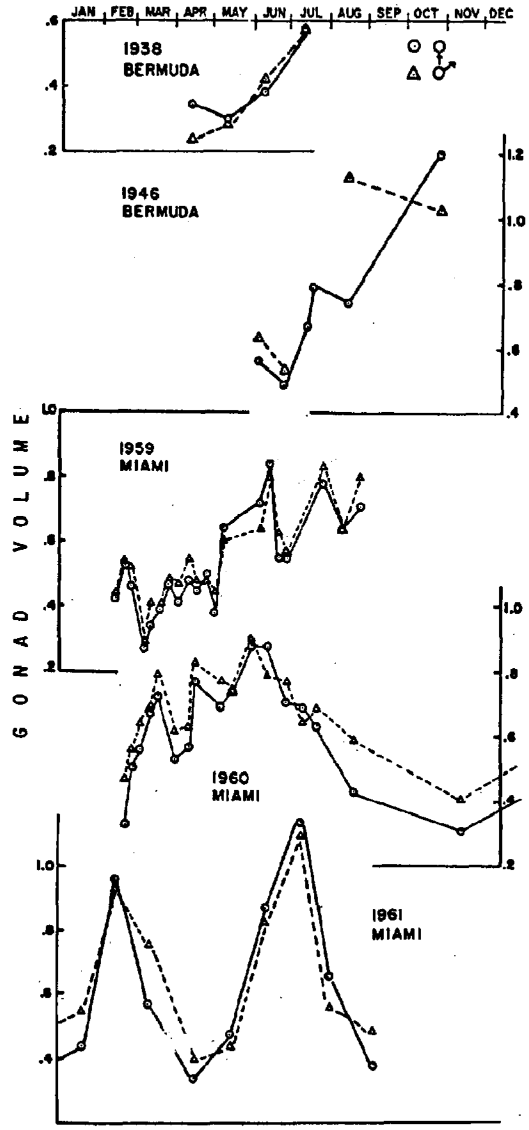
Growth of known year groups from Bermuda (1937-19
from the Miami area.

Fig. 22A. Growth of urchins (Moore et al., 1963).



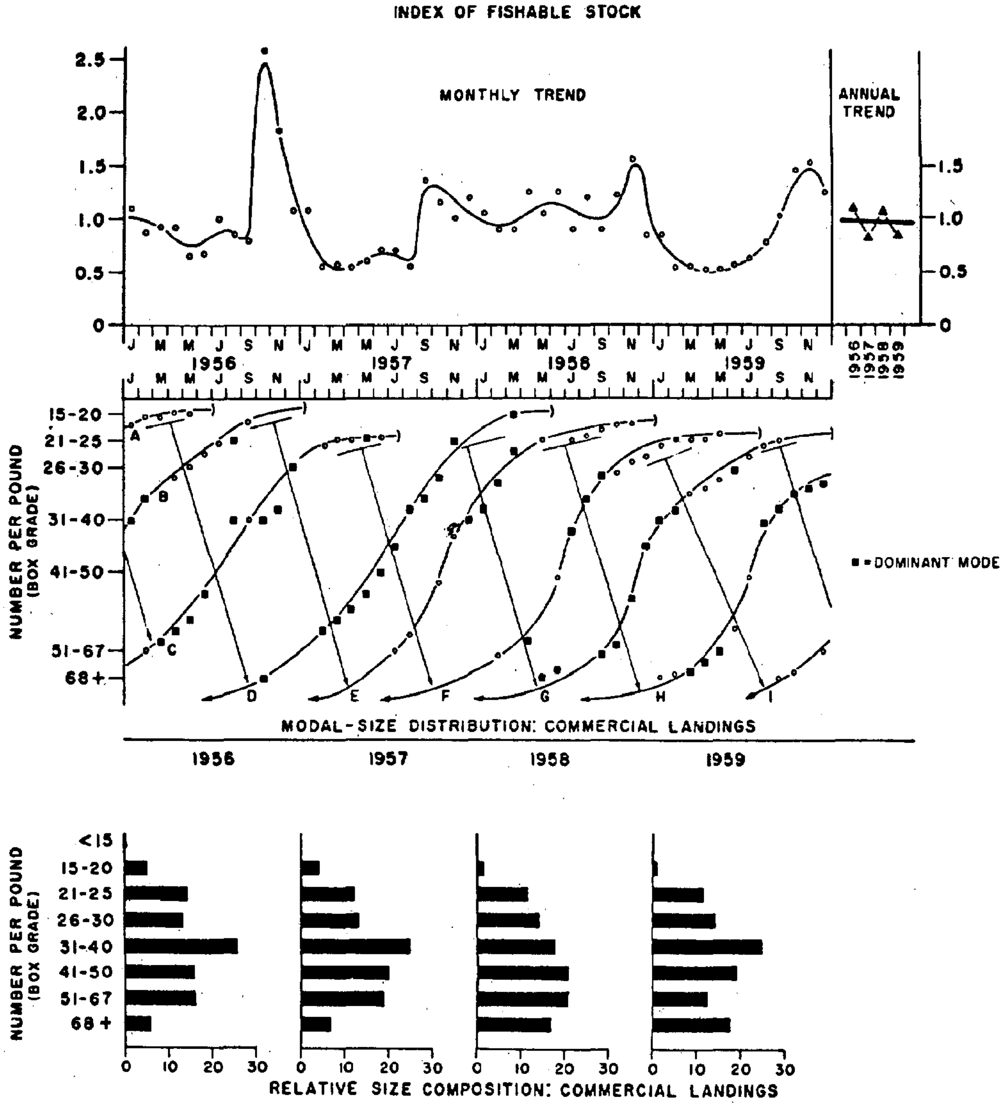
Mean relative gonad volume of the population of *Tripneustes ventricosus* from Virginia Key, Florida, in 1962-63.

Fig. 22B. Growth of urchins (McPherson, 1965).



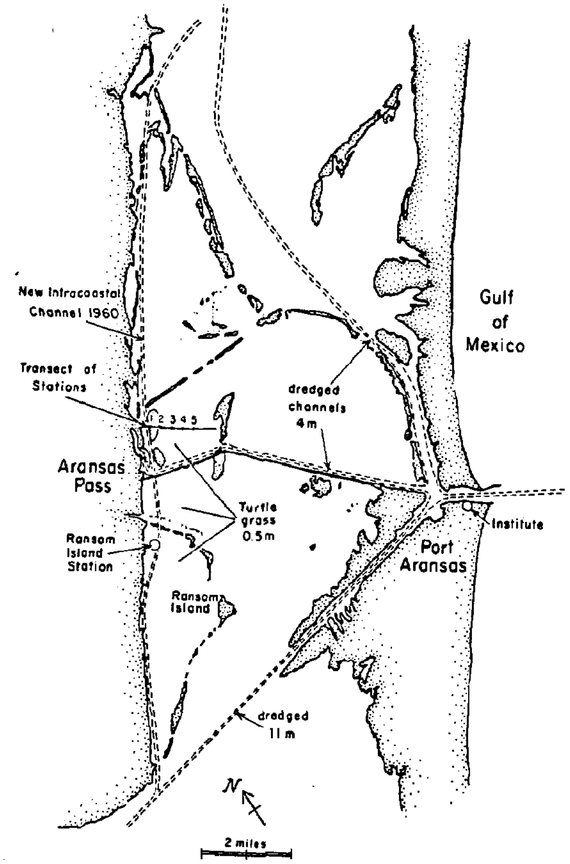
Seasonal changes in gonad volume expressed as $\frac{10.\ \text{Gonad Volume}}{\text{Test Volume}}$ in *Tripneustes*.

Fig. 23. Reproductive cycles in urchins (Moore, Jutare, Jones, McPherson, and Roper 1963).



Analysis of pink shrimp statistics for Sanibel-Tortugas area, 1956-59.

Fig. 24. Seasonal patterns of pink shrimp catch off southwest Florida (Kutkuhn 1960).


New Intracoastal Channel 1960
Transect of Stations
1 2 3 4 5
Aransas Pass
Ransom Island Station
Ransom Island
Turtle grass 0.5m
dredged channels 4m
Gulf of Mexico
Institute
Port Aransas
dredged 11m
N
2 miles

Map of Redfish Bay near Aransas Pass, Texas, indicating the study area, the 5 stations, the intracoastal channel, and the Ransom Island Station.

Fig. 25. **Redfish Bay, Aransas Pass, Texas a shallow area or turtle grass (Odum, 1963).**

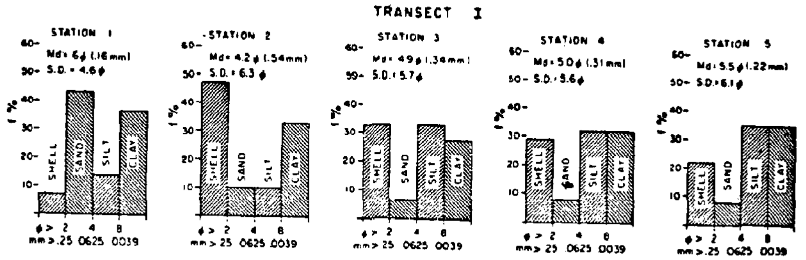
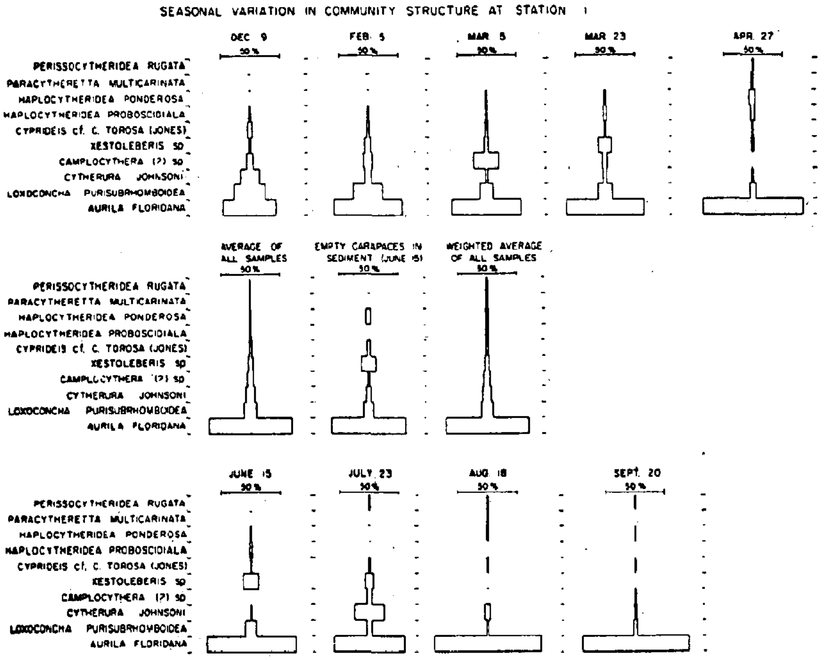
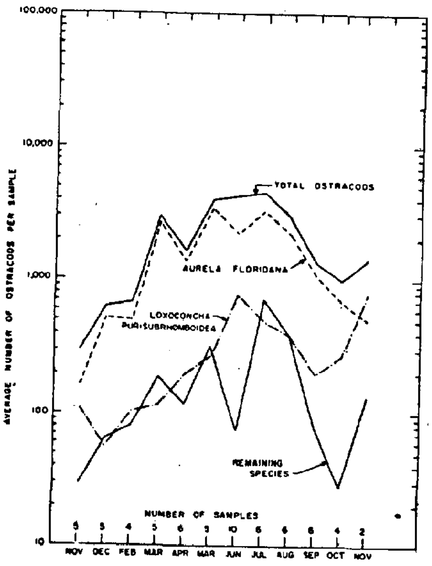


Fig. 26. **Sediment properties in station transect shown in Fig. 25 (Kornicker, 1964).**

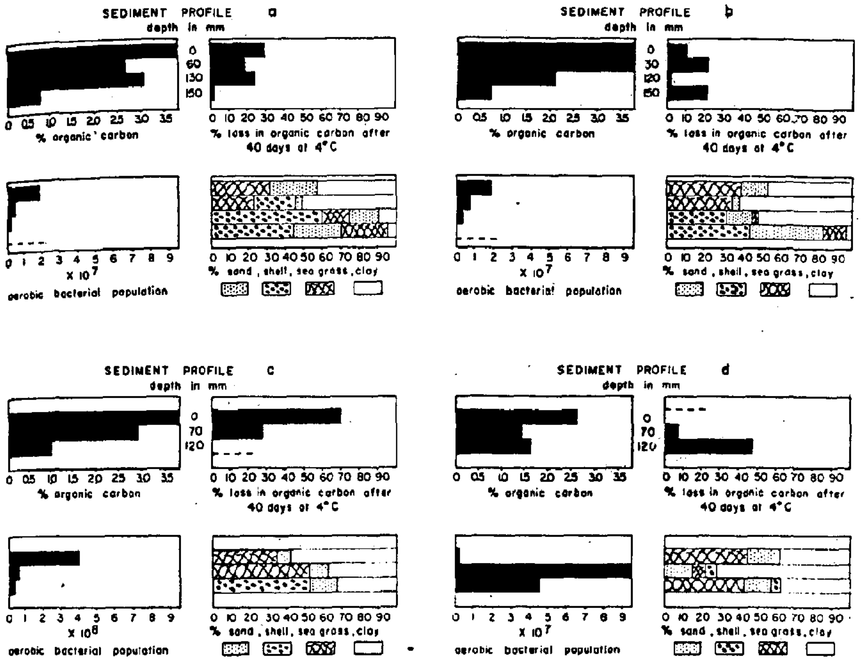


Ostracod population structures in samples from station 1, averaged population structure, and population structures of empty carapaces collected from sediment at Station 1.



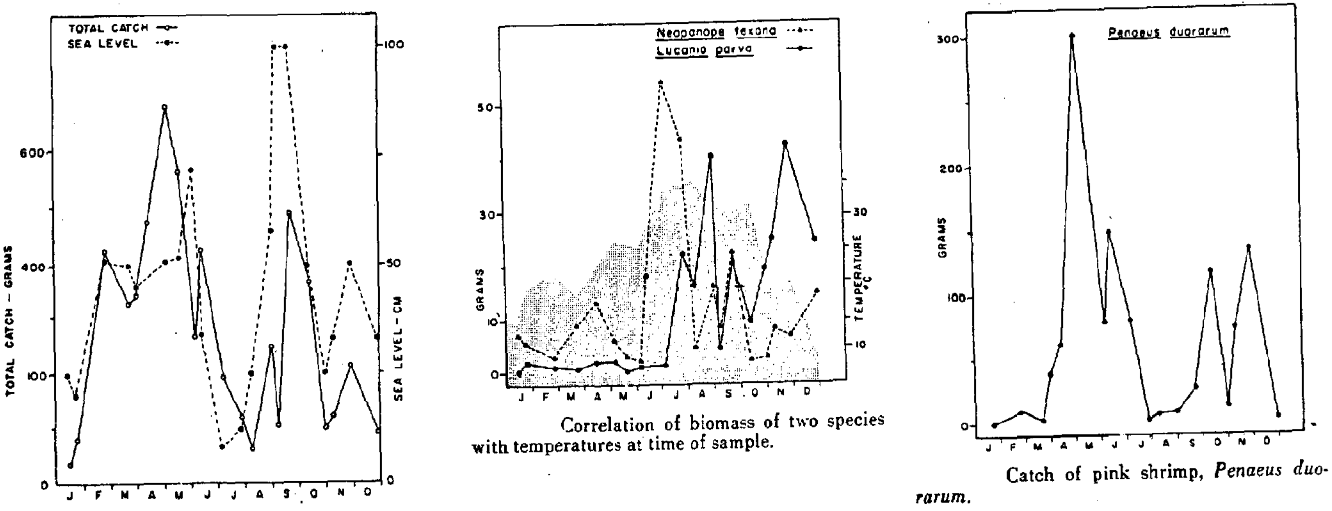
Average monthly abundance of all ostracods, *Aurila floridana*, *Loxoconcha purisubrhomboidea*, and « remaining species » in Redfish Bay. Ostracod abundance based on samples containing not less than 150 specimens.

Fig. 27. Ostracod associations and seasonal distribution in Redfish Bay, Texas (Kornicker, 1964).



Analysis of sediments from station 5 during (a) (b) February, and (c) (d) March 1959.

Fig. 28. Distribution of organic matter and sediments in short cores in turtle grass, Redfish Bay, Texas (Volkmann and Oppenheimer, 1962).

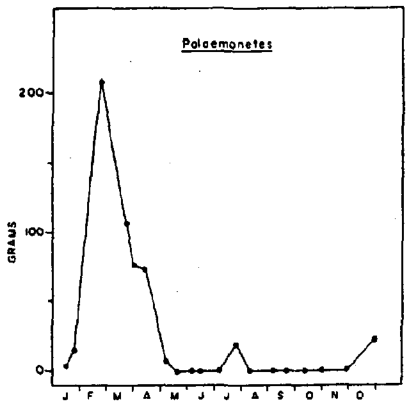


Total biomass (excluding larger species) correlated with bay water level at time of sample. 100 gms = 0.85 gms/m² in all graphs.

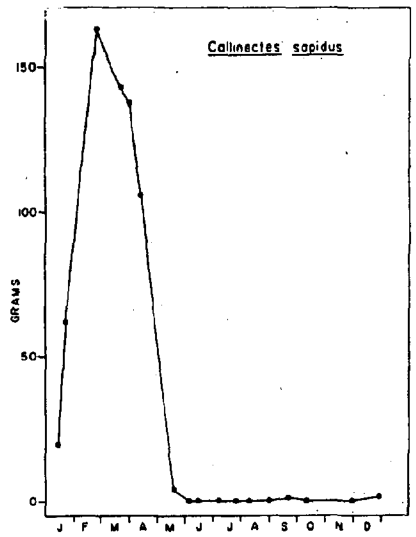
Correlation of biomass of two species with temperatures at time of sample.

Catch of pink shrimp, *Penaeus duorarum.*

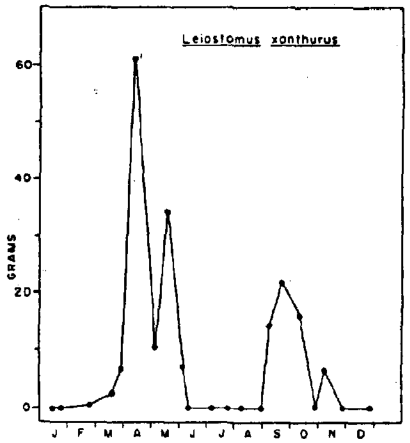
Fig. 29. Seasonal records of biomass with drop net in Redfish Bay turtle grass (Hoese and Jones, 1963).



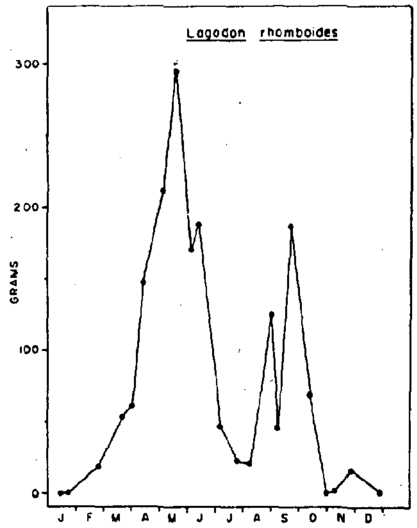
Catch of grass shrimp, *Palaemonetes pugio.*



Catch of blue crabs, *Callinectes sapidus.*



Catch of spot, *Leiostomus xanthurus.*



Catch of pinfish, *Lagodon rhomboides.*

Fig. 30. Stocks of animals in turtle grass, Redfish Bay, Texas (Hoese and Jones, 1963).

Table 19. (Parker, Gibbs, and Lawler 1963).

Summary of chemical analyses

Sample	Co ppm	Fe ppm	Mn ppm
Local bay waters[1]	(5) 0.34—.9	(15) 5—78	(3) 5—15
Redfish Bay sediment	0.4	1000	92
Grass, *Thalassia testudinum*			
root	0.5	366	14
blade	0.34	279	173
Grass, *Diplanthera wrightii*	4.0	735	1100
Mullet, *Mugil cephalus*	0.5	178	18
Pinfish, *Lagodon rhomboides*	0.6	48	24
Fish, *Menidia sp.*	0.6	160	20
Brown shrimp, *Penaeus aztecus*	0.4	75	10
Grass shrimp, *Palemonetes sp.*	2.	285	26
Crab, *Callinectes sapidus*	0.3	166	42
Jellyfish, *Physalia*	1.	....	....

[1] The water concentrations are in parts per billion. The number in parenthesis gives the number of samples between the ranges given.

Table 20. (Parker, Gibbs, and Lawler 1963).

Cobalt, iron and manganese inventory for a grass flat

Sample	Description	Dry weight[1] g/m^2	Co mg/m^2	Fe mg/m^2	Mn mg/m^2
Bay water	1 m depth	1×10^{6}	0.5	30	5
Sediment	per cm depth	1×10^{4}	4.0	1×10^{4}	920
Thalassia	summer crop				
roots		2800	1.4	1×10^{3}	39
blades		200	0.07	74	34
Diplanthera	summer crop	568	2.3	422	627
Mullet	max biomass	2.3	1×10^{-3}	0.4	4
	min biomass	0.06	3×10^{-5}	1×10^{-2}	1×10^{-3}
	avg biomass	0.6	3×10^{-4}	1×10^{-1}	1×10^{-2}
Pinfish	avg biomass	0.18	1×10^{-4}	9×10^{-3}	4×10^{-3}
Crab	max biomass	1.5	5×10^{-4}	3×10^{-1}	6×10^{-2}
Brown shrimp	max biomass	0.07	3×10^{-5}	5×10^{-3}	7×10^{-4}

[1] Dry weight values for animals were taken from Hellier (1962), others were measured.

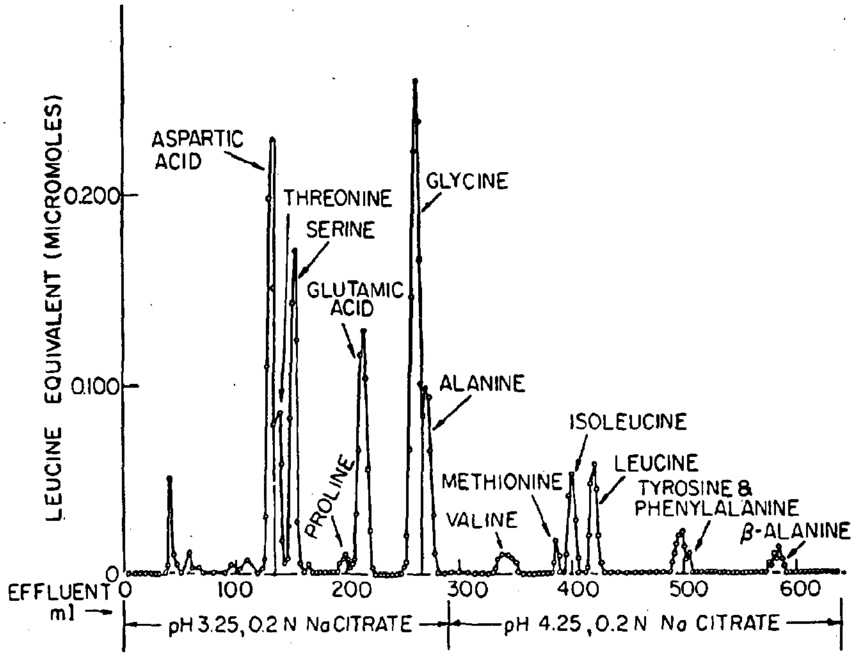
Table 21 (Parker 1962).

Results of zinc analyses

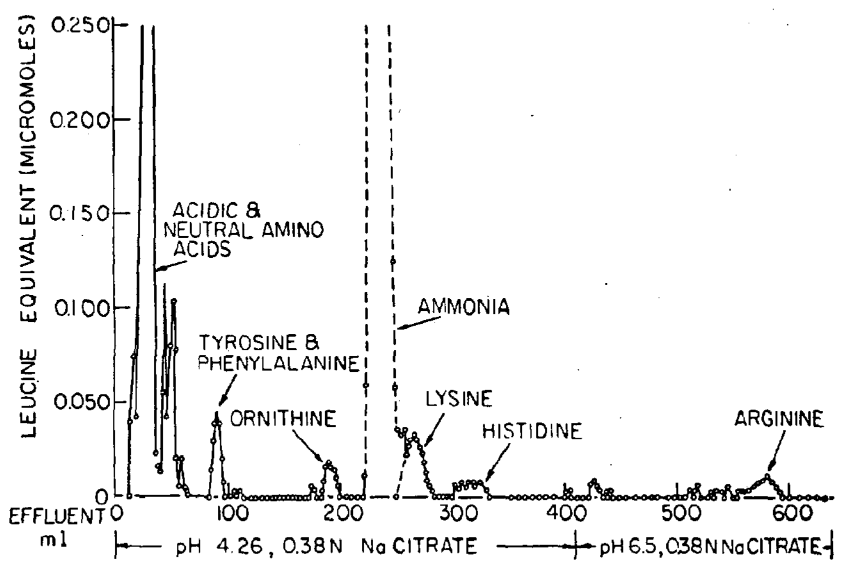
Sample	Description	Zn ppm*
Bay water	salinity 34.4‰, Aug. 18, 1960	0.008
Bay water	salinity 14‰, Dec. 8, 1960	0.006
Sediment	upper 15 cm	10 to 18
Algae	*Digenia simplex*	60
Algae	*Gracilaria sp.*	89
Turtle grass	*Thalassia testudinum*	100
Thin grass	*Diplanthera wrightii*	88
Mullet	*Mugil cephalus*	130
Pinfish	*Lagodon rhomboides*	113
Silverside	*Menidia sp.*	51
Killifish	*Fundulus similis*	29
Croaker	*Micropogon sp.*	43
Brown shrimp	*Penaeus aztecus*	45
Grass shrimp	*Palemonetes sp.*	70
Blue crab	*Callinectes sapidus*	46
Clam	*Chione cancellata*	9
Clam	*Lucinia floridana*	25
Barnacle	*Balanus eburneus*	36

* Average of 3 or more analyses each.

Tables 19-21. Chemical contents of the dominants of a turtle grass bed in Redfish Bay, Texas (Parker, 1962; Parker, Gibbs, and Lawler, 1963).

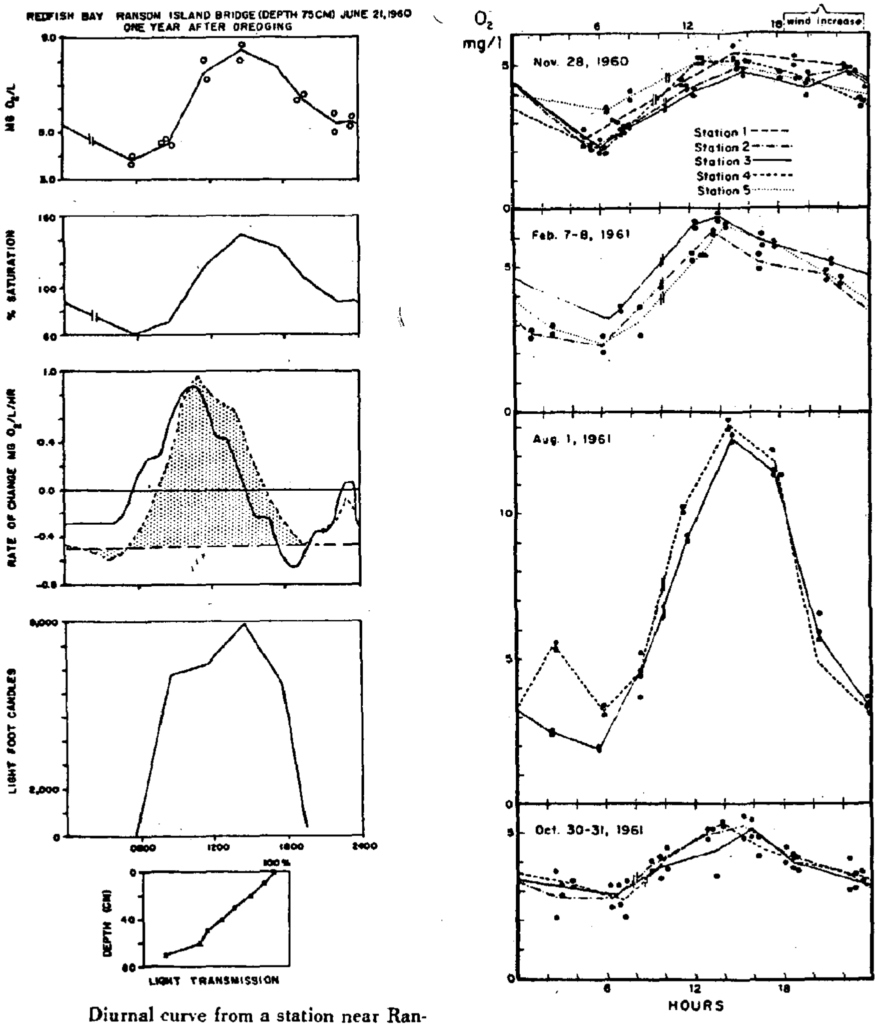


Ion exchange chromatogram of acidic and neutral amino acids. Sample: 15 liters of sea water from Redfish Bay, Texas.



Ion exchange chromatogram of basic amino acids. Sample: 15 liters of sea water from Redfish Bay, Texas.

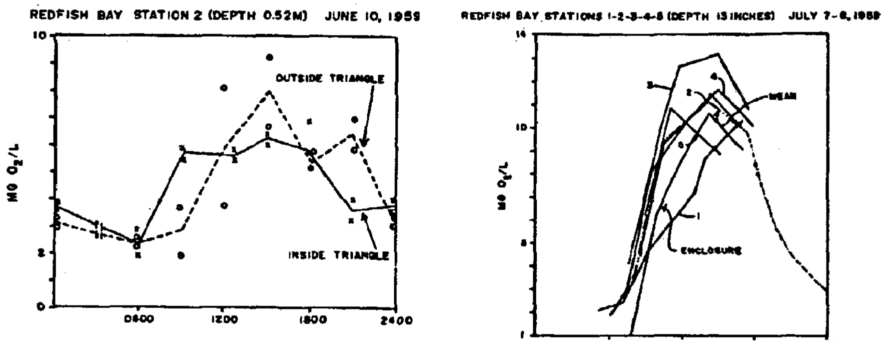
Fig. 31. Amino acids in the waters among the grass blades of meadows of Redfish Bay, Texas (Park, 1963).



Diurnal curve from a station near Ransom Island, June 21, 1960, the summer following the dredging. Vertical transmission of white light with a selenium photometer and frosted glass is provided in the lower graph. Summer graphs like this one show a post-sunset bulge and artifact due to the strong evening sea breeze providing increased aeration not allowed for in the diffusion correction.

Oxygen curves taken at more than one station at the same time. Metabolic figures based on these curves were computed separately and included as points in Fig. 6.

Fig. 32A Diurnal oxygen record of photosynthetic productivity in Texas Turtle grass in Redfish Bay (Odum and Wilson 1962).

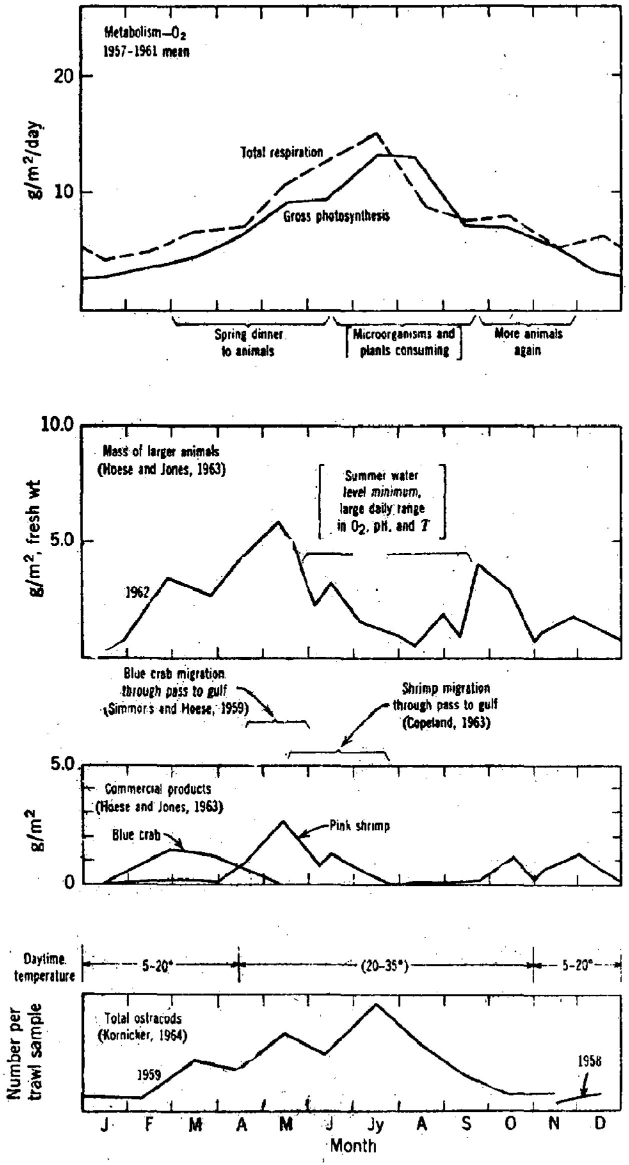


Diurnal curves over turtle grass beds in Redfish Bay inside and outside a fiberglass enclosure, June 10, 1959. Salinity, 28 ‰; depth 0.5 m. Computations based on the inside curve yield: P, 5.9 gm/m²/day; R, 11.1 gm/m²/day. Computations from the outside curve are: P, 6.4 gm/m²/day; R, 11.8 gm/m²/day.

Diurnal curves over turtle grass beds in Redfish Bay inside a fiberglass enclosure and in 5 outside stations July 7–8, 1959. In this figure each point is the mean of two separate Winkler analyses. Salinity, 32.8 ‰.

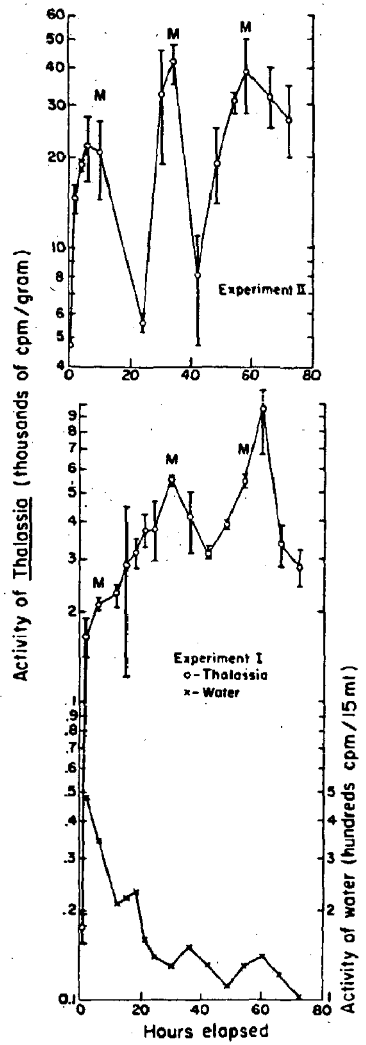
Fig. 32B. Diurnal oxygen records in turtle grass of Redfish Bay, Texas. Left graph, within a fiberglass barrier pen; right graph, on a day with extremely low set of mean tide (Odum and Wilson, 1962).

PART IV. ENERGY TRANSFER

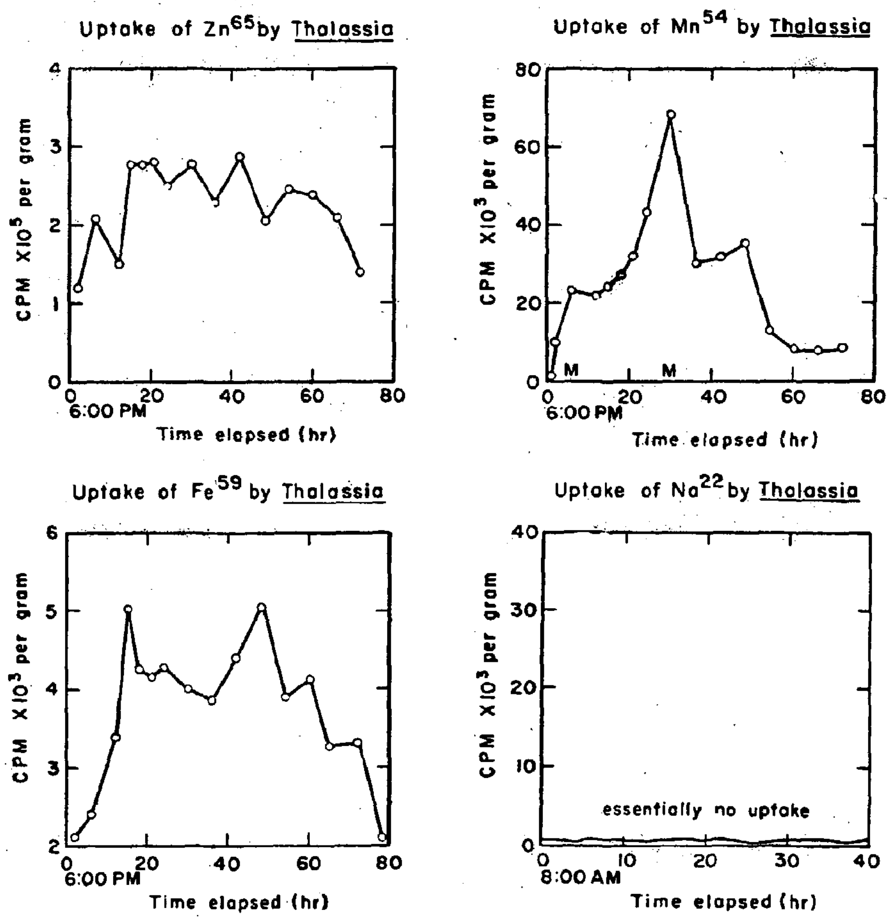


Seasonal changes in photosynthesis, total respiration, and some principal stocks for a turtle grass bed, Redfish Bay, Port Aransas, Texas.

Fig. 33. Seasonal diagram summarizing studies of productivity in Redfish Bay, Texas (Odum, 1967b).



Duplicate experiments showing the uptake of Co-60 by *Thalassia*. Only experiment I shows the loss of activity by the water which was observed in both.



Typical experiments showing the uptake of Zn-65, Mn-54, Fe-59 and Na-22 by *Thalassia*.

Fig. 34. Uptake of four radioactive tracers by turtle grass (Parker, 1966).

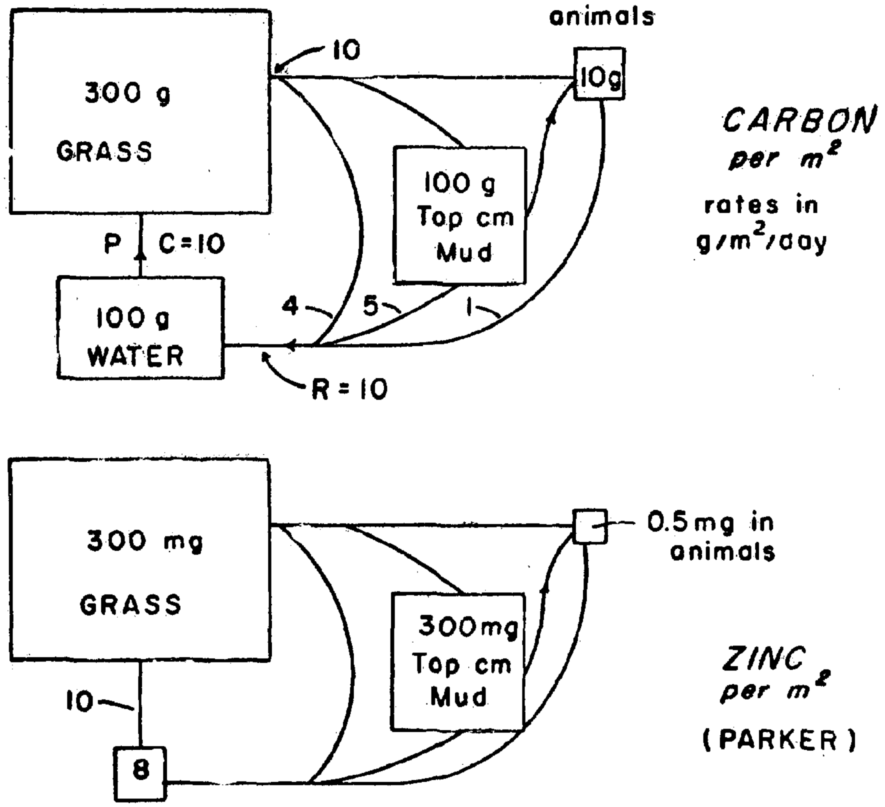
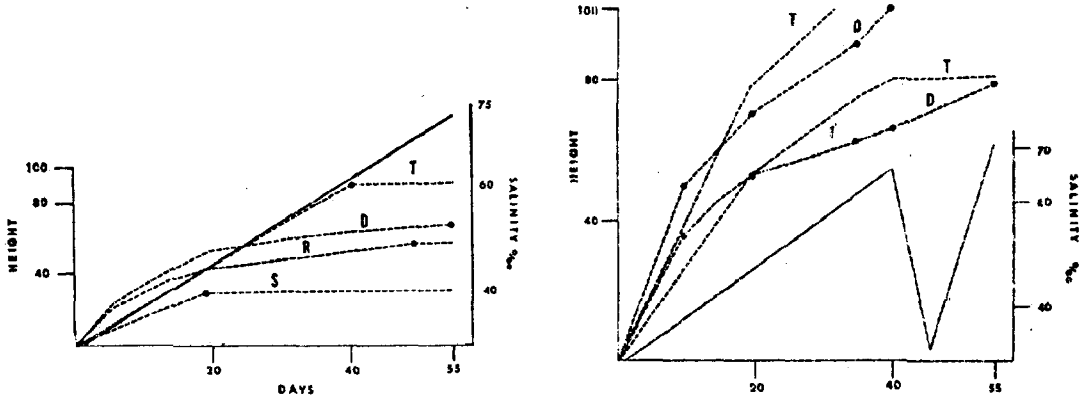

animals
300 g
GRASS
10
10g
CARBON
per m²
rates in
g/m²/day
100 g
Top cm
Mud
P
C=10
100 g
WATER
4
5
1
R = 10
300 mg
GRASS
0.5mg in
animals
300mg
Top cm
Mud
ZINC
per m²
(PARKER)
10
8

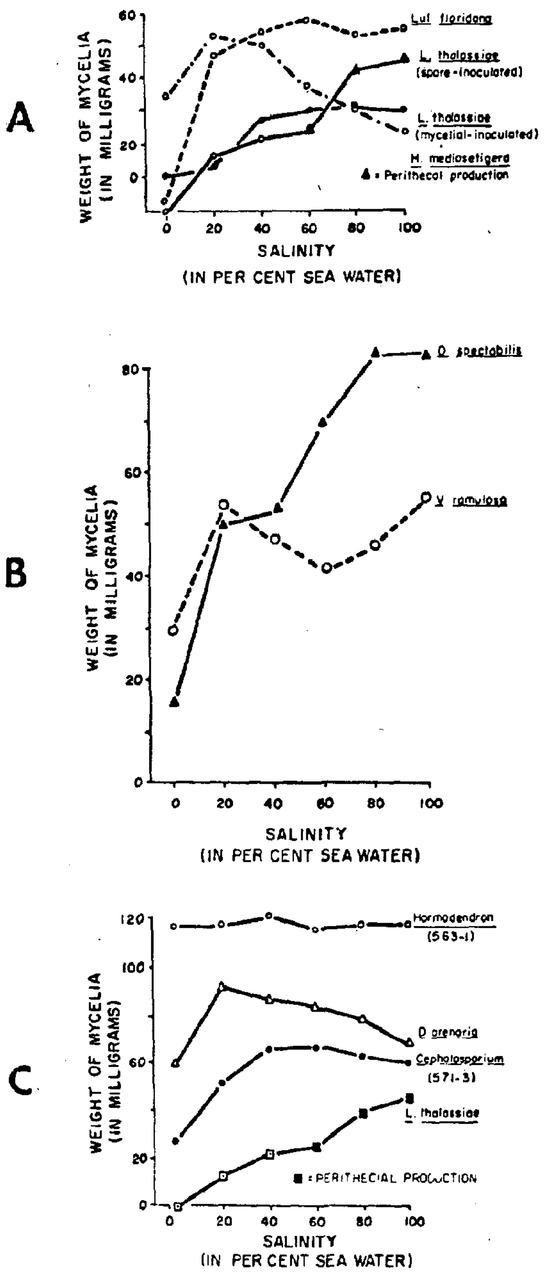
Fig. 35. Mineral cycling diagrams for carbon and zinc in Texas turtle grass (Odum, 1963).



Comparison of average accumulated height (cm) for four marine spermatophytes: T (*Thalassia*); D (*Diplanthera*); R (*Ruppia*); S (*Syringodium*) to increasing salinity in a temperature-controlled tank. The dot on a growth curve approximates the position at which height increase terminated. The salinity at that time is indicated on the solid line.

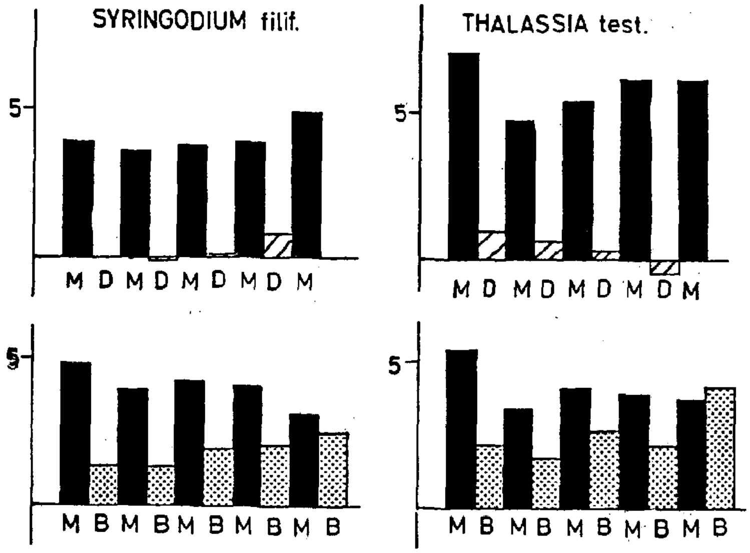
Comparison of average accumulated height (cm) for *Thalassia* (T) and *Diplanthera* (D) to seawater and to increasing salinity in outdoor concrete ponds. Height in the seawater pond (top two lines) is shown only to 100 cm. The salinity decrease after 40 days was due to a 4-in. rain. Salinity is indicated by the solid line.

Fig. 36. Growth of bottom plants as a function of salinity (McMillan and Moseley, 1967).



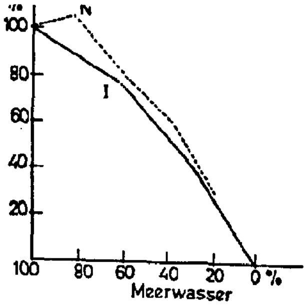
Growth response of selected marine fungi to various concentrations of seawater, expressed as "% seawater." (Obtained by appropriate dilution of natural seawater, salinity 36-37 0/00, with distilled water). (A) ascomycetous species. (B) Deuteromycetes with variously modified spores. (C) foliicolous fungi from turtle grass.

Fig. 37. Growth of marine fungi associated with turtle grass as a function of salinity (Meyers 1968).



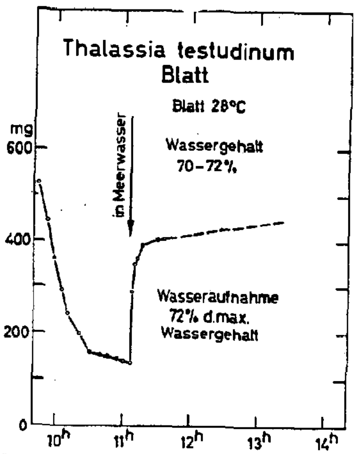
Photosyntheserate der marinen Phanerogamen *Syringodium filiformis* und *Thalassia testudinum* aus dem karibischen Meer bei 30minütigem Wechsel des Mediums. M: Meerwasser, D: destilliertes Wasser, B: $\frac{n}{1000}$ KHCO$_3$-Lösung

Fig. 38. Comparison of bottom plant growth in low salinities where dilutions were made with distilled water containing bicarbonates needed for photosynthesis (Hammer, 1968).



Photosyntheseraten von *Thalassia testudinum* in verschiedenen Salzgehalten. I: identisches Material; N: jeweils neues Material. Die Expositionszeiten betrugen 30 min pro Verdünnungsstufe. Abszisse: wie Abb. 3. Ordinate: Photosyntheseraten

Fig. 39. Decline of turtle grass photosynthesis with decreasing salinity (Hammer, 1968).



Thalassia testudinum: Gewichtsabnahme in Luft; Gewichtszunahme in Wasser

Fig. 40. Water uptake properties of leaves of turtle grass after exposure (Gessner, 1968).

shows the carbonate content of the diluting freshwater sharply affecting the ability of the plant tissue to maintain a net energy budget under stress of freshwater application. Gessner (1968) finds exposed Thalassia able to take up water rapidly due to epidermal adaptations (Fig. 40). Hypersaline conditions occur in South Florida (Fig. 21) as well as South Texas. Fuss (1967) found turtle grass growing faster than Diplanthera (Table 22), in running sea water tanks.

Temperature Adaptations

The generally poor ability of tropical animals to acclimate to temperature changes was established as early as 1914 by Mayer. The economy of functions achieved by not carrying temperature adaptations may contribute to the ability to do other functions that maximize the success of species and associations where temperature regulation is already provided.

Seasonal Patterns

The pattern of seasonal variation in tropical meadow systems is most marked at the northernmost range The record of photosynthesis and respiration in a turtle grass bed in Texas is given in Fig. 33 as determined with diurnal oxygen measurements. Data on individual days have nearly a 10 fold range (Fig. 32) in activity from the cloudy dark short days of winter to the long sunny days of summer. The total community activity as indicated by the respiration measurements (Fig. 33) stays closely in phase by movements of populations, by the effects of temperature in accelerating micro-organismic activities, and by the automatic dependence and consequent systems coupling of respiration to the accumulations of organic matter in the previous time period.

Seasonal patterns in similar latitude but under more uniform light and temperature are given by Jones (1968) for Virginia Key near Miami (Fig. 16-17), showing some correlation of productivity and seasonal light pulse. Whereas spring flowering and fall fruiting of the turtle grass corresponds to periods of photosynthetic maxima, reproduction in fungi is maximal at the Fall decline of the long season of higher energy input (Meyers, 1968; Fig. 12).

Tropical Meadows under Disturbance

The maps of McNulty (1961) for Biscayne Bay, Miami, Florida, show zones of bottom vegetation (Fig. 41) and associated animals at increasing distances from outfall of domestic sewage and other waters flowing out from shore, including ground water. Near the shore and outfall where nutrients are high, waters are colored, more turbid, and the bottom vegetation is mainly absent or has red algae adapted to shade. Diplanthera and Halophila appear next; and Thalassia appears well awav from salinity and nutrient disturbance. For other properties see Chap. C-6 and E-1.

As a result of dredging and release of turbid waters in Redfish Bay, Aransas Pass, Texas, the grass was killed when smothered 30 cm under silt, but was stimulated to greater growths in the remaining part of the year where the settling sediment did not bury the blades. See Chap. E-4, Table 3, which contrasts chlorophyll in bottom plants in relation to this disturbance.

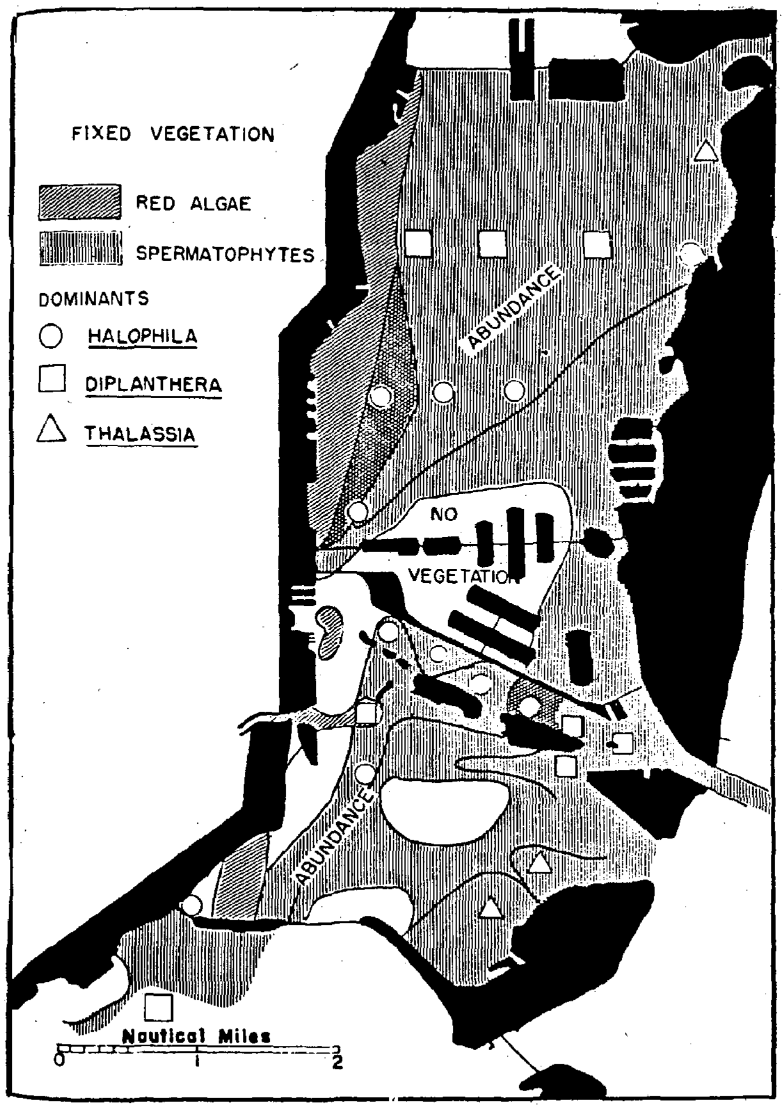
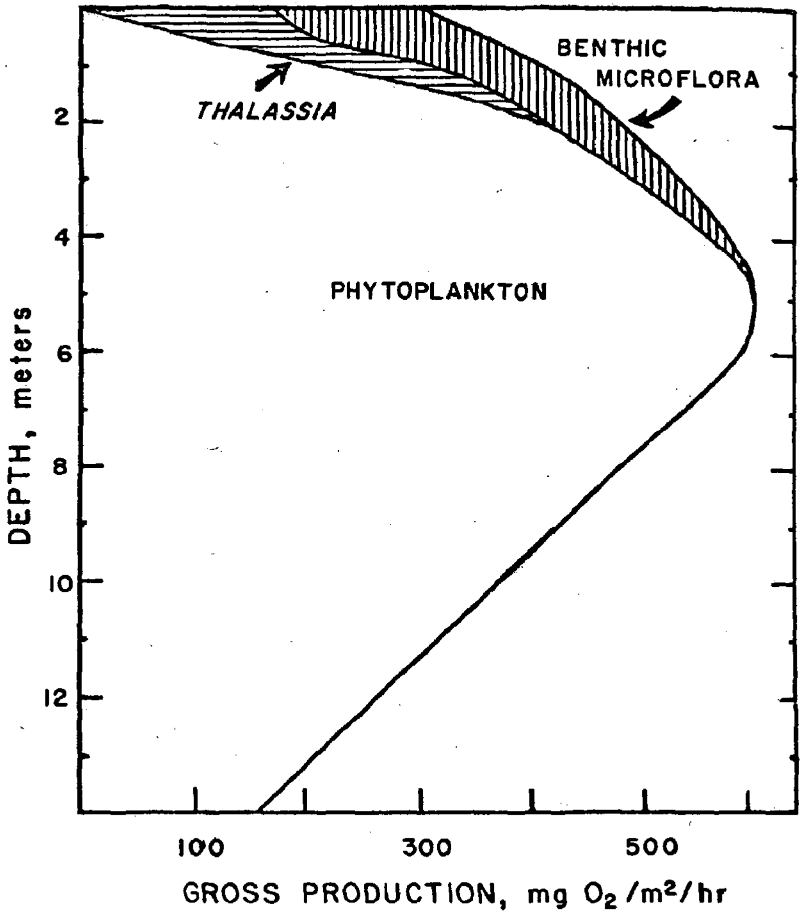

FIXED VEGETATION
RED ALGAE
SPERMATOPHYTES
DOMINANTS
HALOPHILA
DIPLANTHERA
THALASSIA
ABUNDANCE
NO VEGETATION
ABUNDANCE
Nautical Miles
0
1
2

FIGURE 7. Horizontal zonation of fixed vegetation.

Fig. 41. Bottom vegetation in Biscayne Bay, Florida in the vicinity of sewage waste outfall (McNulty, 1961)



Variation with depth of the relative primary production of the plant populations in Boca Ciega Bay. Most of the bay is less than two meters deep.

Fig. 42. Components of photosynthesis in an arm of Tampa Bay, Florida where grass is thin (Pomeroy, 1960).

In Fig. 42 Pomeroy (1960) reports the partition of primary productivity between phytoplankton and sparse turtle grass and its epiphytes.

System Competition and System Hybrids

The benthic vegetation system has means for competition with coral reef systems in those zones where both might otherwise grow. In Puerto Rico in relatively low energy areas, the benthic vegetation intermingles with corals. The ability of the bottom vegetation to outgrow and shade out the coral polyps is balanced by influences of benthic urchins which derive protection from hard coral structure. In conditions intermediate between the high wave energy coral situations and the lower wave energy vegetation bottoms, some mutual organization produces combinations.

Randall (1963a)showed that artificial reefs constructed in tropical meadows developed fish populations that moved out from the refuge,cutting back the benthic vegetation in the near perimeter. This behavior may be a case of the general role of higher consumers in concentrating on members of alternative community systems with the effect of being an agent in system competition.

When waters are deeper and more turbid the benthic vegetation becomes a minor subsystem of the plankton system above, but in shallow clear waters, the benthic system holds plankton components as minor subsystems of its own predominant pattern. An example documenting the low productivity from the dilute grassy bottom under more turbid water is given by Pomeroy (1960) in Fig. 42.

Van Breedveld (1966b) used submerged grass, Syringodium filiform, on tomato plants in Florida comparing its effects on growth and its chemical analysis with those of a brown alga. Table 23 shows analyses of the plants which accounts for their success as a fertilizer. Salt was no problem since it washed away in that particular climate. Anderson (1960) used data from the Texas turtle grass to estimate potential yields for agricultural uses.

Overall Energy Budget

Brylinsky (1967), working with R. J. Beyers, attempted computations of an energy flow for the turtle grass community in Texas with the results in Table 24. They are comparable to those of temperate zone Zostera beds worked out by Peterson (See Chapter C-7 and the diagram in Fig. 37).

Research Needs

Many questions are unanswered and require direct experiments. For the main classes of wastes from urban development, what is the total system response of the tropical meadows? Does plankton blooming develop and shade out the bottom system; is the benthic system stimulated or set back? How much simplification takes place in the system that might channel food production? Which wastes, if any, are compatable with high gross productions of tropical meadows?

Table 22. Winter survival of sea grasses (Fuss 1967)

Weight and percentage of living sea grasses recovered 6 and 8 months after planting in trays suspended in an open sea-water system

Genus and period	Wet weight planted (9/1-3/65)	Plant material recovered	
		Wet weight	Percentage
Thalassia:	Ounces	Ounces	Percent
6 months....	28.0	22.4	80
8 months....	28.1	16.8	60
Diplanthera:			
6 months....	5.3	0.9	17
8 months....	5.3	0.1	2

Table 23. Analyses of Syringodium used for fertilizing tomato plants (van Breedveld, 1966b).

	June, 1964	July, 1964	Norwegian Ascophyllum
Nitrogen, %	1.610	1.890	1.57
Phosphorus, %	0.857	0.676	0.21
Potassium, %	1.16	-	1.28
Iron, %	0.053	0.106	0.09
Copper, %	0.0032	0.00252	0.00635

Table 24. Summary of production and respiration for turtle grass community of Redfish Bay, Texas. Figures are expressed in kcal/m^2 · yr (Brylinsky, 1967).

Trophic Level	Production	Respiration
Producers	8876	3076
Herbivores		370
Carnivores		1273
Detritivores		2491
Export (net prod.)		44
Total	8876	7254

Chapter B-4

TROPICAL INSHORE PLANKTON SYSTEM

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Characteristic tropical inshore plankton associations occur in shallow waters along tropical and subtropical coasts where the ecosystem is not subjected to regular seasonal temperature pulses. With less controlling influence from seasonal factors more complicated biological interactions develop than in temperate systems. The chief energy inputs are light and organic matter from adjacent areas, such as mangrove swamps. The waters are deep enough so that plankton predominates over bottom plants but shallow enough that the bottom is involved in the mineral cycle.

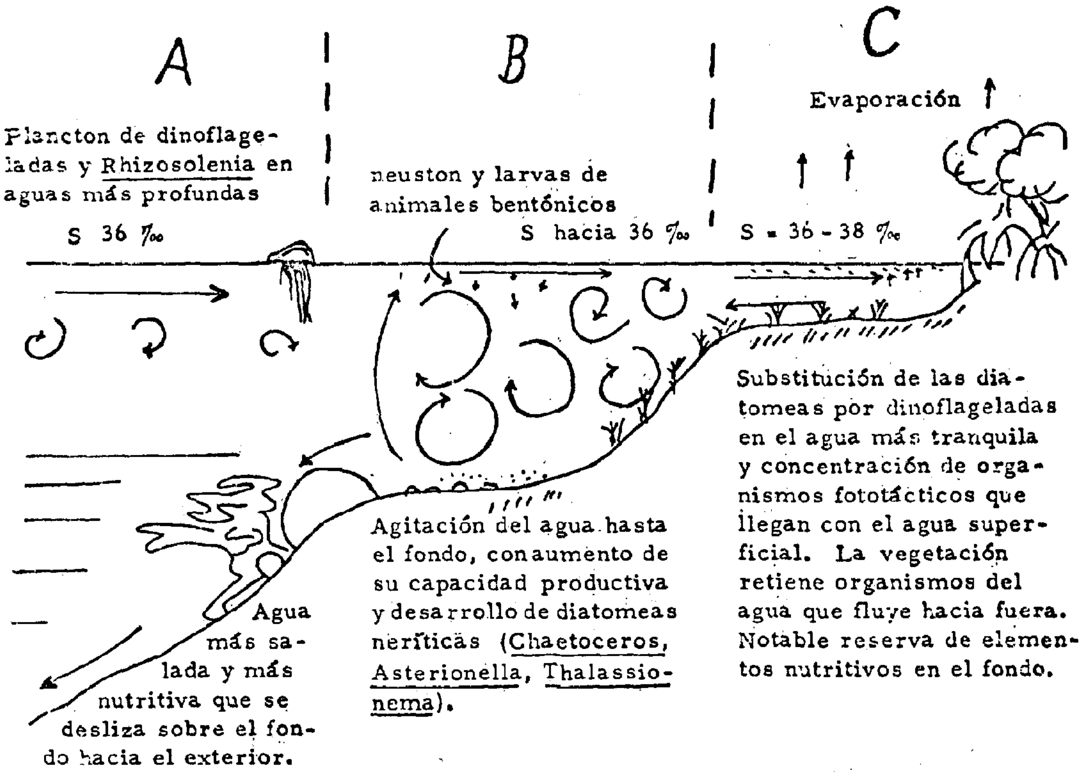
Plankton communities achieve maximum stability in certain small, shallow bays of dry regions where there is a notable lack of influence by tides, waves, or sudden runoff of fresh water. Each of these bays contains a discrete water mass with a slow renewal rate. The community achieves the steady state characteristic of an ecological climax. Tropical bays with indigenous plankton communities are rather uncommon in the United States and elsewhere.

EXAMPLES

Figure 1, taken from Margalef (1962), shows the ecosystems in a generalized cross section perpendicular to the southern coast of Puerto Rico. The deeper offshore waters have the characteristics of blue water coasts. In the shallower waters there is no vertical stratification and the waters are mixed all the way to the bottom. Nutrients and organisms are not permanently lost from the euphotic zone. There is extensive exchange with the blue-water regions, and oceanic salinities prevail. However, there is a characteristic phytoplankton community with Chaetoceras, Asterionella, and Thalassionema. In many of the enclosed and semi-enclosed bays salinities build up because of high evaporation rates and low fresh-water input. Nutrient levels are high and indigenous ecosystems develop. Figure 2 is a general map of the inshore waters of southwestern Puerto Rico and shows areas where tropical plankton communities have been studied.

Bahía Fosforescénte

A remarkable example of the stable plankton bays is Bahia Fosforescénte on the southern coast of Puerto Rico. This bay has a permanent bloom of the dinoflagellate Pyrodinium bahamense which is responsible for the brilliant bioluminescence of the bay every night of the year. Any disturbance in the



Plancton de dinoflageladas y Rhizosolenia en aguas más profundas

neuston y larvas de animales bentónicos

Substitución de las diatomeas por dinoflageladas en el agua más tranquila y concentración de organismos fototácticos que llegan con el agua superficial. La vegetación retiene organismos del agua que fluye hacia fuera. Notable reserva de elementos nutritivos en el fondo.

Agitación del agua hasta el fondo, con aumento de su capacidad productiva y desarrollo de diatomeas neríticas (Chaetoceros, Asterionella, Thalassionema).

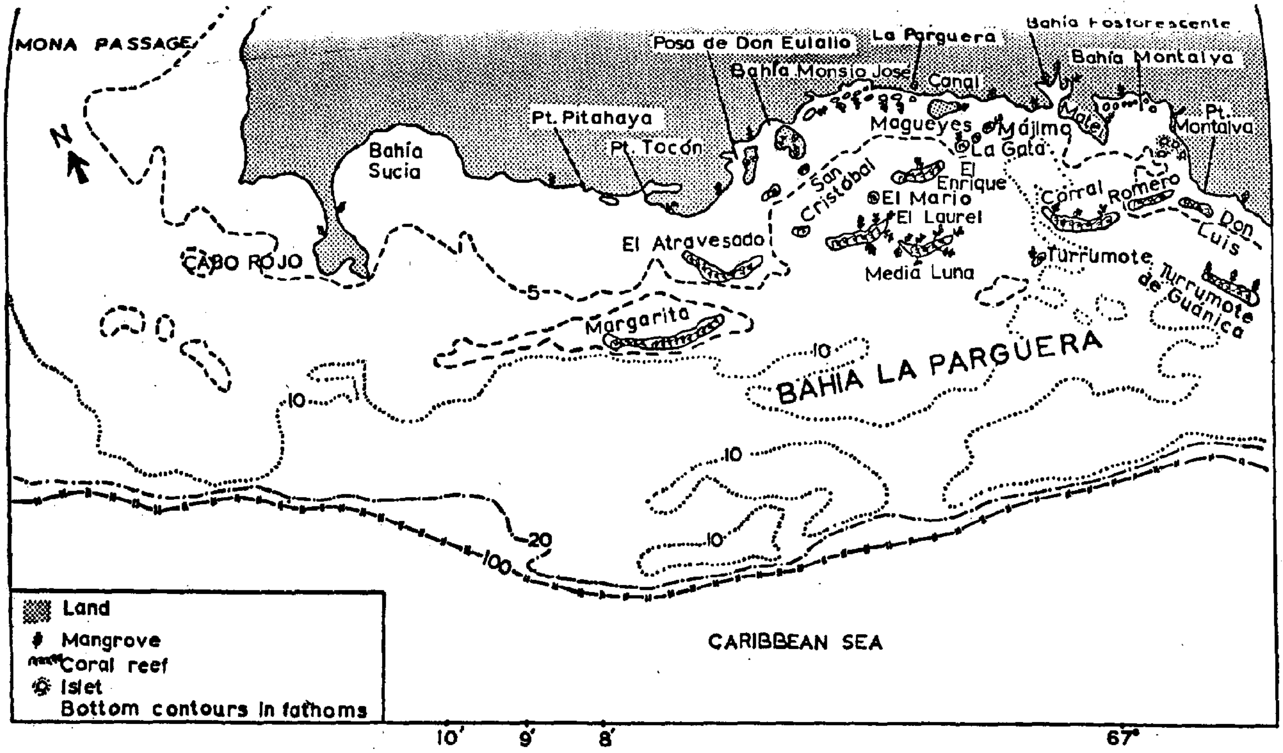
Agua más salada y más nutritiva que se desliza sobre el fondo hacia el exterior.

Plankton composed of dinoflagellates and Rhizosolenia in the deeper waters. Salinity 36 ppt. More saline and nutrient-rich water sliding seaward along the bottom.

Neuston and larvae of benthic animals. Salinity about 36 ppt. Circulation of water all the way to the bottom, increasing the productive capacity and favoring neritic diatoms (Chaetoceras, Asterionella, Thalassionema).

Evaporation. Salinity 36-38 ppt. Replacement of diatoms by dinoflagellates in the quieter waters and concentration of the photosynthetic organisms which migrate into the surface waters. Vegetation retains organisms from the outflowing water. Prominent reservoirs of nutrient elements in the bottom.

Fig. 1. Tropical inshore areas in a generalized cross section perpendicular to the southwest coast of Puerto Rico (From Margalef 1962; p. 392).


MONA PASSAGE
N
Posa de Don Eulalio
La Parguera
Bahía Fosforescente
Bahía Monsio José
Canal
Bahía Montalva
Pt. Pitahaya
Pt. Tocón
Bahía Sucia
Magueyes
Májimo
La Gata
Mateí
Pt. Montalva
San Cristóbal
El Enrique
El Mario
El Laurel
Corral
Romero
Don Luis
El Atravesado
CABO ROJO
Media Luna
Turrumote
Turrumote de Guánica
5
Margarita
10
BAHIA LA PARGUERA
20
100
Land
Mangrove
Coral reef
Islet
Bottom contours in fathoms
CARIBBEAN SEA
10'
9'
8'
67°

–Southwest coast of Puerto Rico, showing region where plankton samples were collected.

Fig. 2. Map of the southwest coast of Puerto Rico (From González and Bowman 1965).

water agitates these single-celled organisms and stimulates them to give off light; as long as they are undisturbed there is no bioluminescence. The wakes of boats, the outlines of swimmers, and the paths of frightened fishes are marked by the flashing displays of thousands of disturbed dinoflagellates. Often the light may be bright enough to read by. Even raindrops striking the water produce thousands of momentary flashes all over the bay. The bay represents not only a pleasing esthetic experience for visitors with a sense of wonder but also a unique opportunity for ecologists to study climax in a natural plankton community, a concept of widespread interest. Bioluminescence is common in other temperate and tropical waters, but conditions favorable for this phenomenon are usually transitory and unpredictable.

Physical conditions in Bahía Fosforescénte are rather constant. Burkholder and Burkholder (1958) observed surface temperatures at various stations ranging from 28.5° to 30.5°C in July. Values at these same stations in February averaged 3.4°C lower. Bahía Fosforescente lies in a rain shadow and receives very little runoff from the surrounding land area. Such rainfall as does occur is primarily seasonal. Because of low runoff and high evaporation rates salinities are high. Coker and González (1960) reported surface values ranging from 34.1 to 36.7 parts per thousand. Values go higher in the upper fingers of the bay among the mangroves. Figure 3 shows salinities in a typical vertical section observed by Margalef (1962). Figure 4 shows the vertical section after a rain when a less saline tongue of water entered the bay at its surface and sank beneath the incoming waters at the mouth.

Another significant factor is the relatively small exchange with the open sea. Tidal amplitudes are small, a third of a meter or less. There is only one tidal cycle per day. The mouth is shallow and is narrow in relation to the size of the bay. Exchange of water through the mouth is thus extremely restricted, and an ecological climax is maintained without physical interference. Coral reefs lying offshore further protect the bay by cutting down on wave and current action.

There is little vertical stratification in the bay since it is shallow enough for continuous mixing. The average depth of Bahía Fosforescénte is 3.5 meters, and the maximum depth is about 4.5 m. There is oxygen all the way to the bottom, and the top part of the sediments is aerobic.

Along with the physical constancy there is a characteristic set of chemical and biological factors. Most of Bahía Fosforescénte has a gray-green to brown coloration markedly different from the clear blue waters offshore. In shallow peripheral zones the waters are dark brown, probably because of mangrove peat on the bottom. Inorganic and organic nutrients are undoubtedly contributed from the surrounding watersheds during the rainy season. Because of its slow rate of water exchange the bay acts as a nutrient trap which maintains a characteristic set of chemical conditions.

Organic nutrients build up beyond the levels ordinarily found in flushed estuaries. Burkholder and Burkholder (1958) reported levels of Vitamin B_{12} in the suspended matter of Bahía Fosforescénte ranging from 430 to 2930 $m\gamma$ per gram of dried solids, higher than in waters outside the bay. (See Table 1). These levels were also higher than in other estuarine ecosystems which have been studied. Values for dissolved B_{12} were 3.0 and 3.5 $m\gamma$ for 2 stations in the bay and 1.3 $m\gamma$ for a station outside the bay.

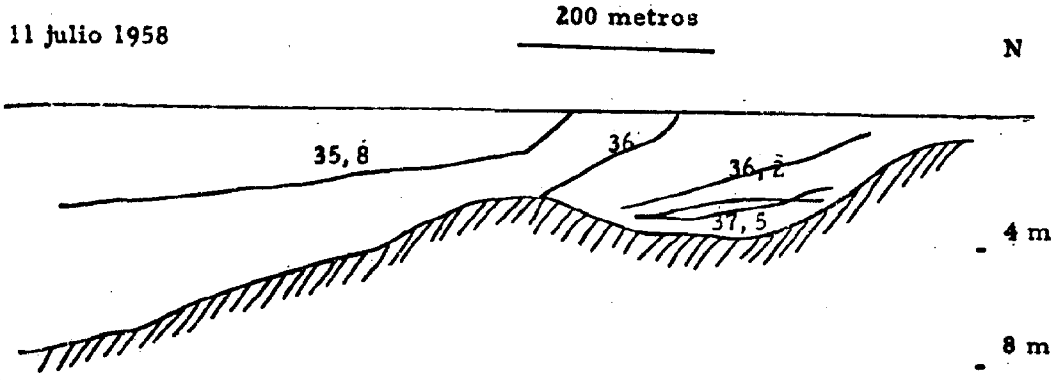

11 julio 1958
200 metros
N
35, 8
36
36, 2
37, 5
4 m
8 m

Fig. 3. Cross section of Bahía Fosforescénte and adjoining waters outside of the bay, showing isohalines (From Margalef 1962; p. 389).

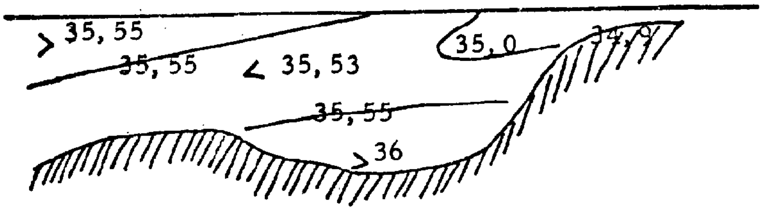

> 35, 55
35, 55
< 35, 53
35, 0
34, 9
35, 55
> 36

Fig. 4. Cross section of Bahía Fosforescénte showing isohalines after fresh water runoff following a rain (From Margalef 1962; p. 391).

Table 1. Vitamin B_{12} in suspended solids of Bahía Fosforescénte. Stations 3A, 4A, 6A, and 10 are in the open waters of the bay. Station 7A is in the mouth, and Stations 8A and 9A are in the waters outside the bay. Other stations are around the margins of the bay (From Burkholder and Burkholder 1958).

VITAMIN B_{12} IN SUSPENDED SOLIDS ASSAYED WITH *E. coli.*
DATA ARE GIVEN IN mγ PER GRAM OF DRIED SOLIDS AND PER LITER OF WATER

Station	Depth in feet	B_{12} per gram		B_{12} per liter	
		Surface	Bottom	Surface	Bottom
1A	1	847	847	7.3	7.3
2A	4	932	430	7.2	20.0
3A	4	1313	693	8.8	17.5
4A	12	1041	882	5.0	40.0
6A	12	1325	780	8.8	73.3
6 (muddy)	12	1690	1264	100.0	146.7
7A	12	891	588	5.3	36.7
8A	14	909	833	3.3	2.5
9A	12	1875	1667	2.5	2.5
10	13	1100	1099	14.7	86.7
13	6	2930	2400	40.0	40.0
16	8	1071	—	12.0	—
22	3	625	865	15.0	23.3
25	5	1010	940	10.3	23.3
26	5	954	910	13.7	23.3

It is known that dinoflagellates similar to those found in Bahía Fosforescênte require Vitamin B_{12} and thiamin, but the nutritional requirements of these specific dinoflagellates are not known. The Burkholders thought that synthesis of the B vitamins probably occurred at significant physiological levels within the bay itself but stated that vitamins were undoubtedly contributed from the surrounding watershed as well. They suggested that contribution from the fringing mangroves was likely.

A characteristic phytoplankton community is found in Bahía Fosforescênte. There is a dominance of dinoflagellates, with diatoms playing a much less important role than in most estuaries. The dinoflagellate Pyrodinium bahamense (Fig. 5) is responsible for most of the bioluminescence. Other species of dinoflagellates commonly found in Bahía Fosforescênte, though in lesser densities, are Dinophysis caudata, Peridinium divergens, P. oceanicum, and Ceratium furca. Margalef (1961b) listed a total of 16 species of dinoflagellates and 6 species of diatoms found there. Burkholder, Burkholder, and Almodôvar (1967) reported that blooms of Cochlodinium sp. sometimes occurred and gave a red color to the water in the upper arms at the western end of the bay. These blooms generally seemed to occur after heavy rains and were readily destroyed by motorboats passing through them. Chlorophyll a values in the open waters of the bay were 4.5 - 5.4 mg/m^3 and reached 37 mg in the Cochlodinium blooms (Fig. 6 and Table 8).

While this bay may contain respectable standing crops of phytoplankton its primary productivity is not remarkably high. Burkholder et al. (1967) used the carbon-14 technique and found an average of 45 mg carbon/m^3/hr (C/m^3/hr) fixed in the open waters of Bahía Fosforescênte, intermediate between the average of 5 mg in the nearby open sea and values ranging up to 900 mg in certain bloom situations in the surrounding waters. Cochlodinium blooms in the western arm of the bay had productivities ranging from 55 to 182 mg C/m^3/hr (Fig. 7; Table 2). Plankton samples from the bay enclosed in bottles showed increasing phytosynthesis with increasing light intensity up to 51,000 lux, the maximum intensity attainable in the experimental apparatus of Burkholder et al. (Fig. 9). Odum, Burkholder, and Rivero (1959) studied the primary productivity of Bahía Fosforescênte and nearby areas using diurnal oxygen curves and light- and dark-bottle techniques. They reported that 24-hour respiration of bottle samples exceeded photosynthesis in most areas of the bay; this means that there had to be an import of organic matter, probably from the mangrove areas. Gross photosynthesis was reported as 1.40 g O_2/m^2/day. Photosynthesis of the bay waters was relatively small in comparison to nearby coral reefs and turtle grass flats.

Zooplankton does not appear to be noticeably different from that of other estuarine types. Coker and González (1960) reported after a year-long study of Bahía Fosforescênte that copepods dominated the zooplankton. The predominant species was found to be Acartia tonsa, the same species which is the most common in Long Island Sound. Other dominant species in Bahía Fosforescênte were Oithona minuta, O. simplex, and Paracalanus crassirostris. Coker and González thought that conditions were perhaps less favorable for zooplankton in the bay than in nearby waters. They noted the absence of any large predator species in the daytime plankton but reported that the large copepod Pseudodiaptomus comes out at night. They observed clear seasonal cycles only in O. simplex and

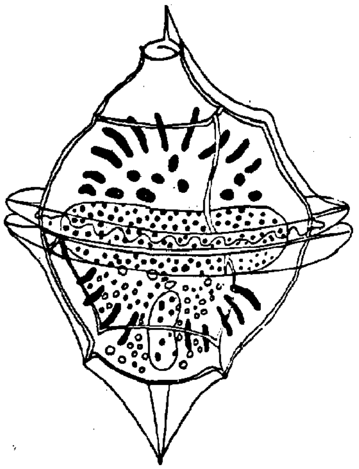
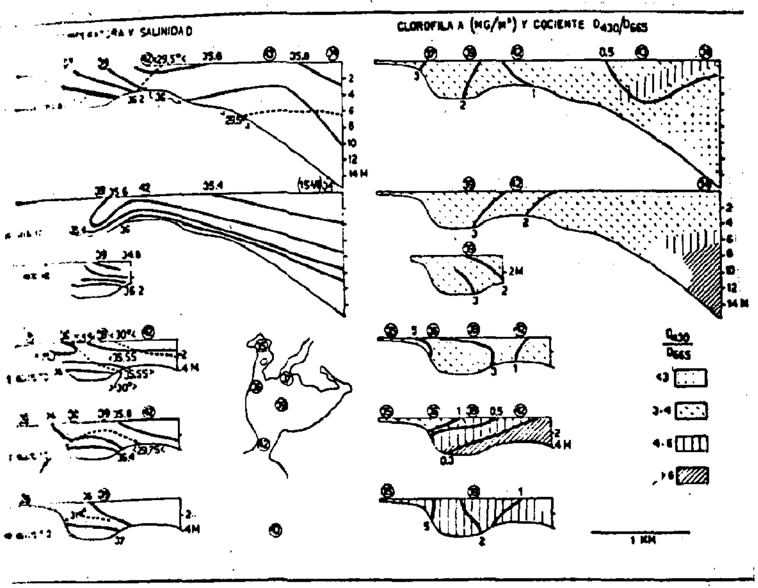


Fig. 5. Pyrodinium bahamense (From Clarke and Breslau 1960).



— Secciones a través de la Bahía Fosforescente y parte de las aguas [illegible] a la misma en distintas fechas (rodeadas por círculos, estaciones 35. [illegible], [illegible], 42, 43 y 84 de fig. 1 y del pequeño mapa incluido en la figura). A la [illegible], distribución de temperaturas y salinidades. A la derecha, distribución [illegible] clorofila a y del cociente entre las densidades ópticas a 430 y 665 milimichas de los extractos acetónicos.

Fig. 6. Cross section of Bahía Fosforescēnte and adjoining waters. Temperature and salinity distributions are on the left. On the right are shown chlorophyll a distribution and the distribution of the ratio of optical density at 430 millimicrons to O.D. at 665 millimicrons, for acetone extracts (From Margalef 1961b).

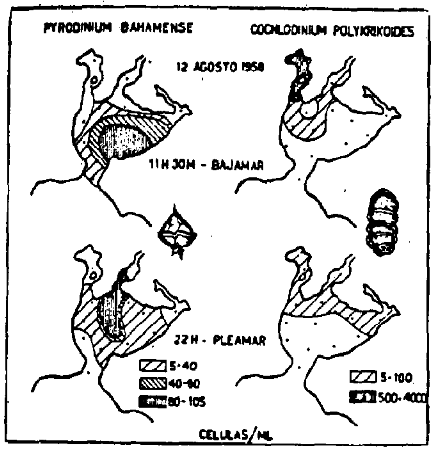

PYRODINIUM BAHAMENSE
COCHLODINIUM POLYKRIKOIDES
12 AGOSTO 1958
11 H 30M - BAJAMAR
22 H - PLEAMAR
5-40
40-80
80-105
5-100
500-4000
CELULAS/ML

Fig. 7. Cell numbers of two species of phytoplankters in Bahía Fosforescênte (From Margalef 1961b).

Table 2. Carbon assimilation by microplankton from Bahía Fosforescênte (From Burkholder and Burkholder 1958).

CARBON ASSIMILATION BY MICROPLANKTON. SURFACE SAMPLES FROM PHOSPHORESCENT BAY IN A FLUORESCENT LIGHT INCUBATOR AT 51,000 LUX

	1963			1964	
	Feb. 23	Apr. 23	May 1	July 10	July 19
			(mg C m^{-3} hr^{-1})		
Center of Bay	30.5	65.0	42.0	28.6	61.5
West Arm	—	54.9	—	182.1	77.3
Outside of Bay	5.5	5.2	6.7	6.8	5.4

Euterpina. Multicellular zooplankton were found to be less diverse than in a nearby bay and in the open water over a reef. Table 3 shows the relative abundance of different zooplankters in these 3 areas. Burkholder and Burkholder (1958) reported an abundant protozoan population but did not give species.

The ecological role of fishes in Bahía Fosforescénte has not been evaluated. Jenkinsia is reported to be abundant, and the paths of light it leaves when fleeing from tourist boats contributes to the esthetic value of the bay. Other forms present are mullets, halfbeaks, and porgies. Fig. 8 shows mollusc data for the Bay.

The high bacterial activity of the sediments is a noteworthy feature. Because there is little vertical stratification in the water, the surface of the bottom muds is aerobic at all times, but anaerobic conditions exist a few centimeters below the surface. Bacterial activity is high both on the surface and in the anaerobic layers. This undoubtedly contributes to the high levels of B vitamins and inorganic nutrients in the water. Burkholder and Burkholder (1958) found the highest B_{12} values in sediments collected from the margins of the bay, especially in the northern areas. They thought that this might be related to microbial activity in decomposing mangrove materials. Aerobic bacteria ranged from 55 to 2400 millions of cells per gram of dried mud. Counts of aerobic and anaerobic bacteria are shown in Table 4. Margalef (1961b) reported pigment values in the sediments of about 2 mg chlorophyll a + b per 100 g.

While light intensity at the surface of the bay is high, up to 130,000 lux, light extinction in the waters is rapid. Coker and González (1960) reported that a 20-cm Secchi disc disappeared at depths ranging from 1.75 to 3.9 m, except for 1 reading of 4.1 m occurring after a heavy rainfall. The Secchi disc always disappeared before reaching the bottom in the open waters of the bay. This is consistent with the finding of Almodóvar and Blomquist (1959) that Thalassia does not grow at depths greater than 2 m in Bahía Fosforescénte.

Burkholder and Burkholder (1958) reported that suspended matter was greater near the bottom than at the surface (Table 5) and increased after a windy period. The winter average (11.2 mg/liter) was higher than the summer average (7.4 mg/l). Suspended matter was composed mostly of plankton. Values were higher in the bay than in the waters outside. They were in the same range as values for Long Island Sound during the spring bloom but lower than figures from waters around Sapelo Island during a bloom. (See Fig. 10.)

Other Puerto Rican Bays

Other bioluminescent bays in Puerto Rico are Bahía Monsio José (Fig. 11), also on the southern coast, and Caño Hondo on Vieques Island. These bays have not been as extensively studied as Bahía Fosforescénte, but physical conditions and biological characteristics are probably similar. Caño Hondo does not lie in a rain shadow but is nevertheless in a very dry region. Bahía Monsio José is the largest of the Puerto Rican bays and has an area of approximately 0.65 hectare.

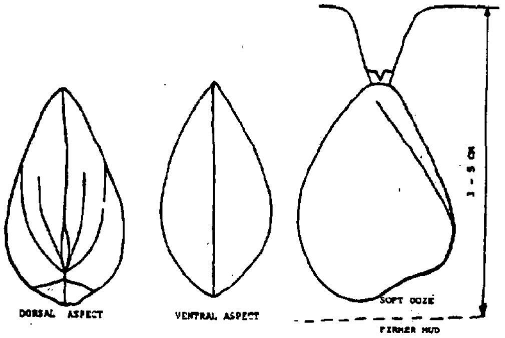
Oyster Bay, Jamaica

Another example which has been studied is the luminescent Oyster Bay in

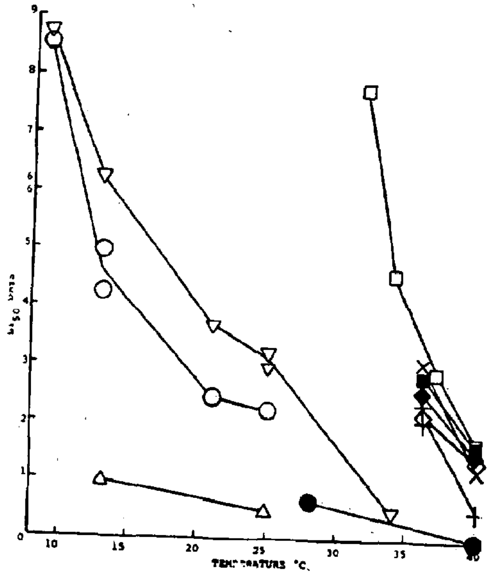
Table 3. Relative abundance of different zooplankters in waters of southwestern Puerto Rico (From Coker and Gonzālez 1960).

Differential distribution by depth for leading zooplankters, showing, for surface and deep at each station, number of collections in which found, mean of percentages for 12 monthly collections, November 1957, to October 1958, and standard deviation of the mean (S.E.)

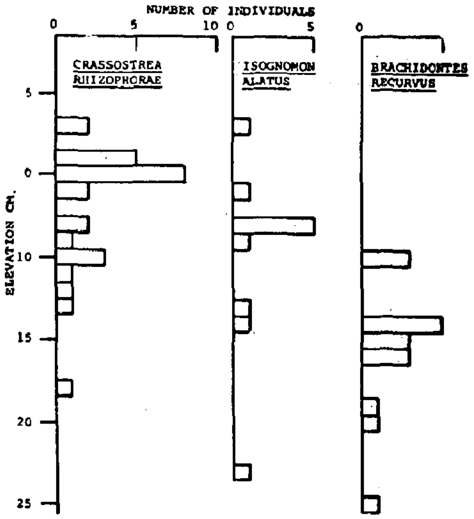
Species	Depth	Bahia Fosforescente			Montalva Bay			Offshore		
		No. Col.	Mean %	S.E.	No. Col.	Mean %	S.E.	No. Col.	Mean %	S.E.
Copepods vs. Other Zooplankton	Surface	12	74.32	5.63	12	62.98	4.55	12	64.77	5.00
	Deep	12	78.35	3.81	12	67.28	3.57	12	62.12	3.41
Oithona minuta	Surface	12	22.60	2.22	12	12.42	2.58	12	6.97	1.16
	Deep	12	18.79	2.25	12	8.88	1.06	12	5.08	0.83
Acartia tonsa	Surface	12	23.43	3.60	8	2.27	0.97	6	0.31	0.12
	Deep	12	10.92	2.08	11	2.33	0.77	1	0.02	0.02
Paracalanus crassirostris	Surface	12	12.20	2.48	12	22.07	5.12	12	26.99	4.77
	Deep	12	10.69	3.09	12	21.28	3.66	12	28.08	3.36
O. simplex	Surface	11	8.30	2.91	12	12.69	1.77	12	8.02	1.56
	Deep	11	7.21	2.18	12	11.83	2.78	12	20.92	3.47
Euterpina acutifrons	Surface	9	0.675	0.19	8	2.08	0.86	11	1.61	0.42
	Deep	9	1.03	0.34	10	2.86	1.13	11	2.40	0.55
A. spinata	Surface	3	0.10	0.05	10	1.82	0.75	9	1.18	0.35
	Deep	3	0.25	0.22	11	3.61	1.71	6	1.39	0.78
O. nana	Surface	3	0.20	0.13	8	1.62	0.53	12	3.15	0.63
	Deep	2	0.05	0.03	10	2.16	1.03	12	2.83	1.04
P. parvus	Surface	3	0.10	0.06	9	1.28	0.33	12	11.93	3.33
	Deep	3	0.19	0.17	7	0.95	0.61	12	3.70	1.42
Larvacea	Surface	12	12.92	3.95	12	6.32	1.73	12	11.52	2.99
	Deep	12	9.74	1.77	12	5.56	1.55	12	7.05	1.00
Univalve veligers	Surface	12	8.52	1.75	12	21.46	3.23	12	11.97	2.81
	Deep	12	8.32	2.55	12	15.75	2.66	12	13.83	3.03
Bivalve veligers	Surface	12	1.78	0.42	12	5.09	1.20	12	3.89	0.86
	Deep	9	1.08	0.36	11	3.86	0.80	11	10.38	2.08
Chaetognaths	Surface	3	0.25	0.17	9	0.60	0.21	12	1.20	0.23
	Deep	2	0.06	0.04	6	0.17	0.07	8	0.47	0.16
Juvenile calanoids	Surface	12	13.84	1.87	12	21.02	3.23	12	17.30	1.63
	Deep	12	24.98	4.30	12	18.35	2.47	12	13.70	1.71
Juvenile cyclopoids	Surface	12	4.70	0.87	12	5.72	1.08	12	8.55	1.42
	Deep	12	9.84	1.91	12	7.13	1.16	12	10.98	1.87
Juvenile harpacticoids	Surface	8	0.91	0.33	8	0.82	0.31	11	1.34	0.63
	Deep	6	0.71	0.28	6	0.95	0.39	11	2.32	0.48
Nauplii, copepod	Surface	12	12.68	3.01	12	14.86	3.26	11	8.68	1.64
	Deep	12	15.21	1.99	12	18.48	4.86	12	6.56	1.30



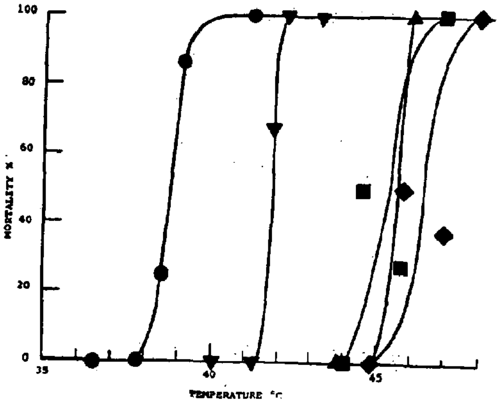
Anomalocardia brasiliana. Shell morphology and position in the substrate.



LT$_{50}$ vs. temperature curves under stagnant conditions for *Lima scabra* ●, *Aequipecten irradians* △, *Modiolus modiolus* ○, *Mytilus edulis* ▽, *Phacoides pectinatus* +, *Crassostrea rhizophorae* ◇, *Isognomon alatus* ◆, *Brachidontes recurvus* ■, *Brachidontes exustus* ×, *Brachidontes demissus* □.



Relative levels of all live individuals of the three species indicated, observed in a period of 80 min. in Bahía Fosforescente. Zero indicates water-level at time of survey.



Mortality-temperature curves for *Lima scabra* ●, *Anomalocardia brasiliana* ▼, *Brachidontes recurvus* ■, *Phacoides pectinatus* ▲, and *Brachidontes exustus* ◆, Exposure time to indicated temperature was 20 minutes.

Fig. 8. Observations on bivalve molluscs from Bahía Fosforescénte. LT$_{50}$ is the time for 50 percent of a population to die (From Read 1964).

Table 4. Numbers of aerobic and anaerobic bacteria in bottom deposits of Bahía Fosforescénte (From Burkholder and Burkholder 1958).

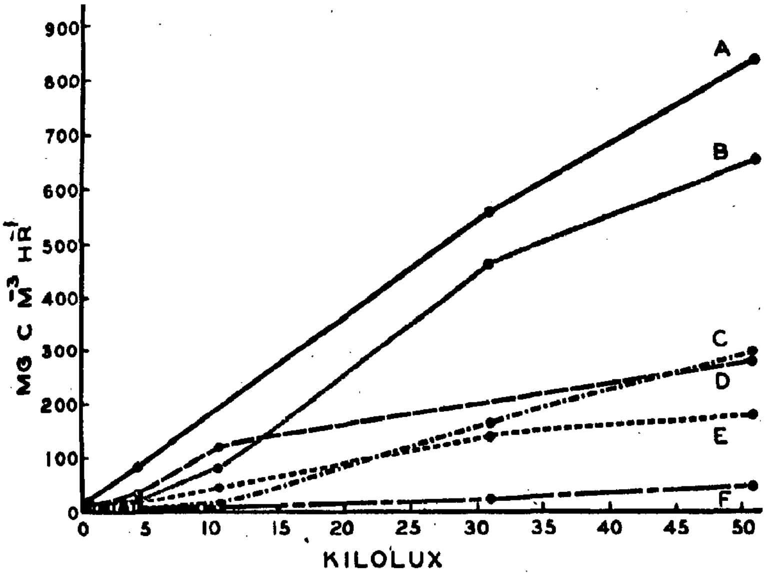
QUANTITATIVE OCCURRENCE OF AEROBIC AND ANAEROBIC BACTERIA IN BOTTOM DEPOSITS OF BAHIA FOSFORESCENTE. DATA ARE EXPRESSED IN MILLIONS PER ML

Station	Aerobic	Anaerobic
10	55	—
32	65	10
25	70	28
19	137	9
31	171	—
9	229	133
3	236	—
23	274	—
11	455	346
22	885	380
13	995	—
28	2440	—

Table 5. Dry weights of suspended solids in Bahía Fosforescénte. Station locations are explained in Table 1 (From Burkholder and Burkholder 1958).

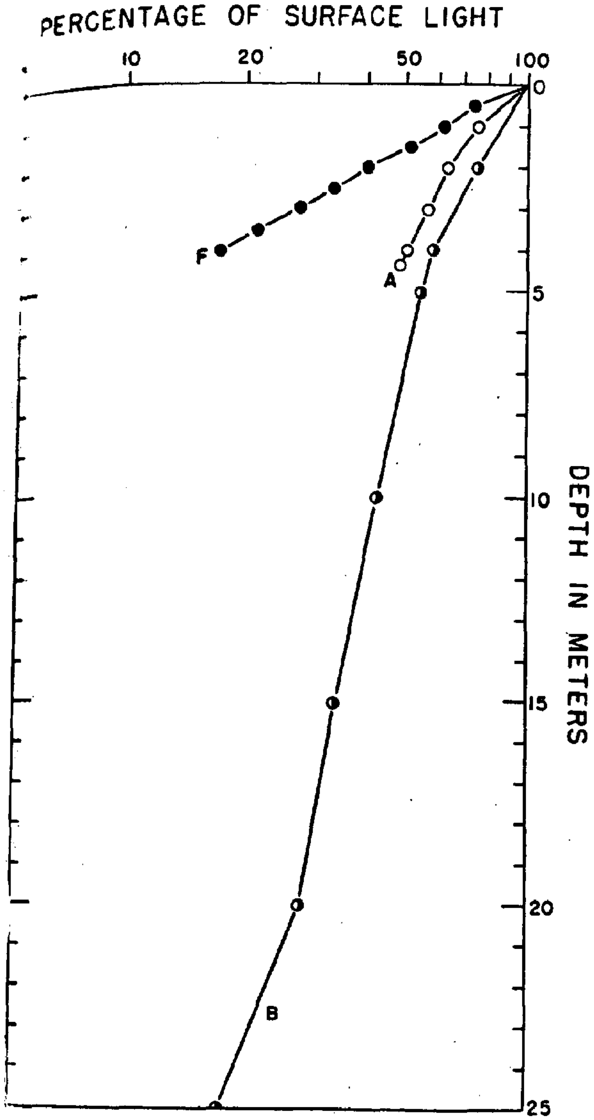
DRY WEIGHTS OF SUSPENDED SOLIDS OBTAINED FROM A SERIES OF STATIONS IN BAHIA FOSFORESCENTE. VALUES ARE EXPRESSED AS MG. PER LITER OF WATER

Station	February Samples		July Samples	
	Surface	Bottom	Surface	Bottom
1A	8.7	8.7	—	—
2A	7.4	46.5	—	—
3A	6.7	35.3	—	—
4A	4.8	45.3	5.6	7.3
5A	7.4	10.7	—	—
6A	6.7	93.5	—	—
6 (muddy)	59.2	116.0	8.6	8.3
7A	6.1	45.2	—	—
8A	3.6	3.0	—	—
9A	1.3	1.5	2.0	—
10	13.3	79.7	—	—
12	—	—	8.9	10.9
13	13.7	16.7	—	—
14	—	—	6.3	9.9
16	11.2	35.5	—	—
22	23.8	27.0	—	—
23	—	—	7.9	7.9
25	10.2	24.5	—	—
26	14.3	25.7	11.9	28.4



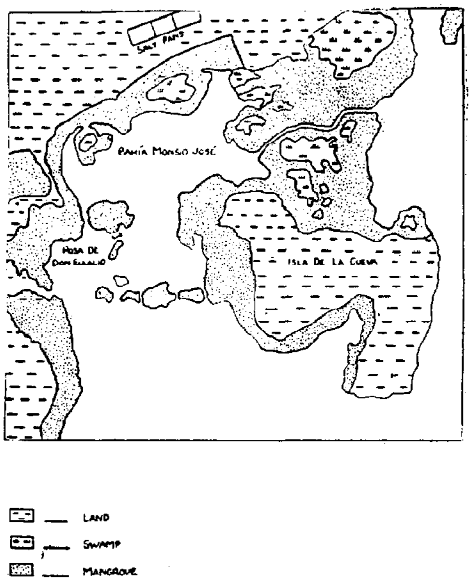
Carbon assimilation by blooms of microplankton in the neritic waters near La Parguera, Puerto Rico.—A, *Goniodoma* sp. bloom at the fish pen, Magueyes Island, Feb. 21, 1963.—B, *Goniodoma* sp. bloom at the eastern end of Magueyes Island, Feb. 19, 1963.—C, Ciliates from the vicinity of sea anemones at La Gata Island, Apr. 24, 1963.—D, Dinoflagellates in a bed of *Thalassia*, at La Gata Island, May 1, 1963.—E, *Cochlodinium* sp. in the western arm of Phosphorescent Bay, July 10, 1964.—F, Mixed plankton in the center of Phosphorescent Bay, Apr. 23, 1963.

Fig. 9. Carbon assimilation by microplankton in the waters of the southwestern coast of Puerto Rico (From Burkholder, Burkholder, and Almodóvar 1967).



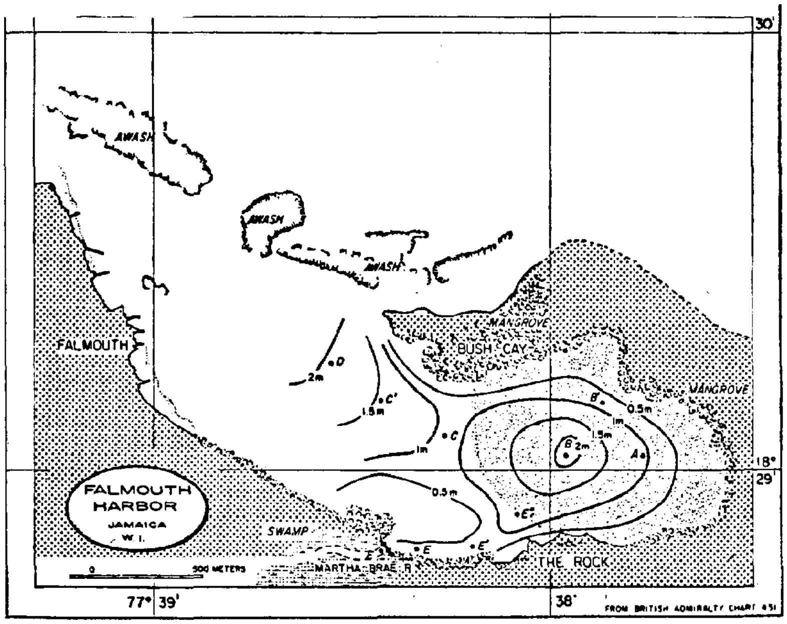
– Transparency measurements : (F) in Phosphorescent Bay, (A) outside at Station A, Feb. 7, 1959, both near noon, bright sun, cumulus clouds, ce 2; and (B) outside reefs at Station B, Feb. 8, 1959, 1400 hrs, bright sun, clouds, wind force 4.

Fig. 10. Water transparency in Bahía Fosforescente and nearby waters (From Clarke and Breslau 1960).


SALT PANS
BAHÍA MONSIO JOSÉ
POSA DE DON EULALIO
ISLA DE LA CUEVA
LAND
SWAMP
MANGROVE

Monsio José Bay and Posa de Don Eulalio

Fig. 11. Bahía Monsio José (From Coker and González 1960).


30'
AWASH
AWASH
AWASH
FALMOUTH
MANGROVE
BUSH CAY
MANGROVE
D
2m
C'
1.5m
C
1m
0.5m
B
A
E
E
E
SWAMP
MARTHA BRAE R.
THE ROCK
18°
29'
FALMOUTH HARBOR
JAMAICA
W. I.
0
500 METERS
77° 39'
38'
FROM BRITISH ADMIRALTY CHART 451

General topography and location of hydrographic stations, Oyster Bay, Falmouth Harbor, Jamaica, West Indies. Approximate limits of brilliant bioluminescence shown with fine stippling.

Fig. 12. Topography of Oyster Bay (From Taylor, Seliger, Fastie, and McElroy 1966).

Falmouth Harbor, Jamaica. Its average depth is 1 m, and the maximum depth is 2 m (Fig.12). The bioluminescent area is separated from the rest of the harbor by a shallow sill. The area is approximately 100 ha.

Inorganic nutrients such as iron and phosphate achieve comparatively high levels, with the iron existing in particulate matter. Taylor, Seliger, Fastie, and McElroy (1966) reported inorganic phosphate values for Oyster Bay of 0.5 - 1.3 micromoles per liter and total phosphorous values of 0.8 - 5.7 micromoles per liter. They found iron concentrations of 1.2 - 11.6 micromoles per liter.

The most noteworthy feature about Oyster Bay is the periodic input of fresh water which it receives from the Martha Brae River, especially after the rather frequent rains. This water spreads out as a layer on the surface and mixes very slowly with the characteristic bay water. Figure13 shows the distribution of surface salinity after two days' rain. Figure14 shows a vertical profile of temperature and salinity both before and after the rain. It is interesting that the bottom waters were about 1° C warmer than the mid-depth waters after the rain. Taylor et al. suggested that this might be due to absorption of solar radiation by suspended matter just above the bottom. Figures 15 and 16 show transects of salinity and temperature across the bay after a rain.

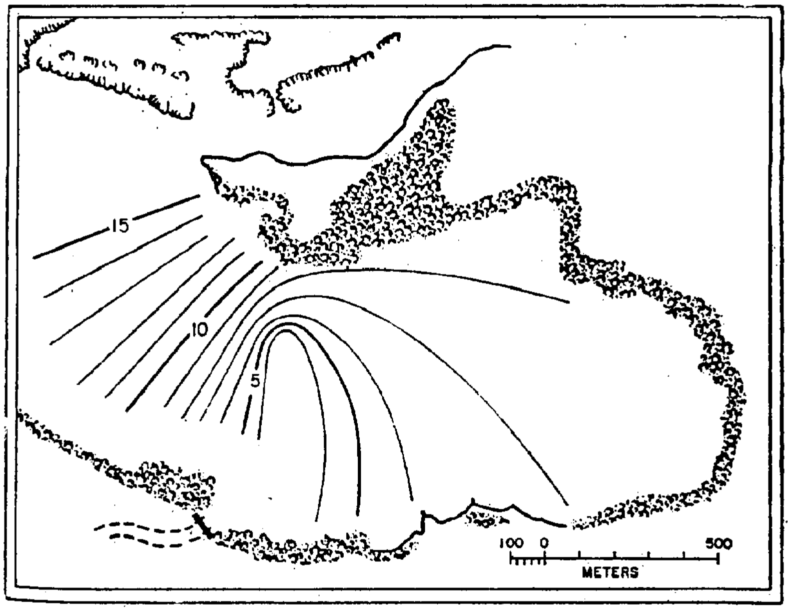
Tables 6 and 7 show cell counts for different phytoplankton species at different stations in Falmouth Harbor, as reported by Taylor et al. Cell densities of up to 200,000 individuals per liter were recorded for Pyrodinium bahamense. After a rainfall stations outside the Oyster Bay sill had relatively high densities of dinoflagellates which had been washed from the bay. Taylor et al. were not sure whether the bay acts as a basin which maintains a slowly reproducing population for a long time or whether it constitutes an environment where rapidly reproducing populations are in equilibrium with the loss of organisms from the bays. They described the diatom populations in the river mouth as a "typical polluted stream" type which became dispersed in the bay (Table 7). The river flows through a rich valley of sugar and banana plantations.

Taylor et al. also observed a diurnal vertical migration in the dinoflagellates. Organisms in the bay moved into the surface layer at night and returned to the lower depths during the day, but there was no movement into the layer of fresh water lying on the surface after the rain (Tables 6 and 8). They also reported a diurnal rhythm of light production. Stimulated luminescence was observed only during the night-time hours, even after the organisms had been kept in constant light for a period of time (Fig. 17).

Carbon-14 productivity values in the bay were consistent with values obtained for Bahía Fosforescente, 11-27 mg C/m^3/hr for samples dominated by dinoflagellates and 87 mg C in a surface sample dominated by an unidentified small diatom.

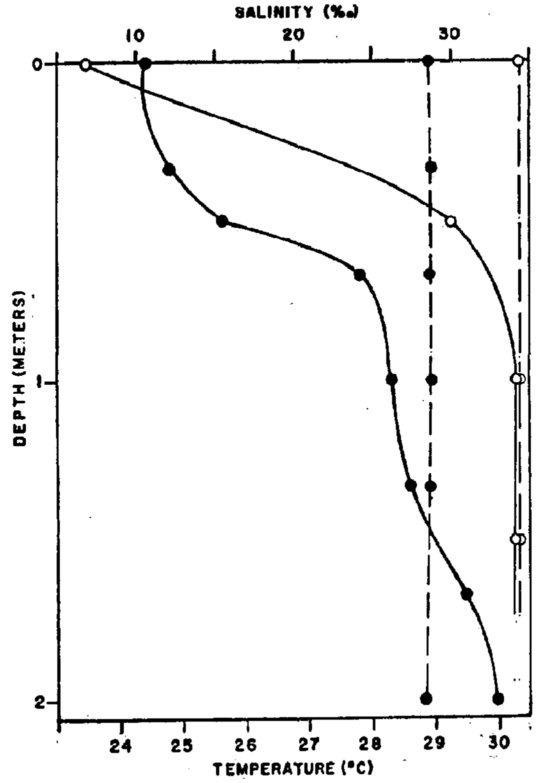
Other Puerto Rican Waters

Information about other inshore areas comes from Margalef (1957, 1961b, 1962), and a few data about these areas have also been included for comparative purposes in bioluminescent bay studies. Margalef (1961b) reported yearly temper-



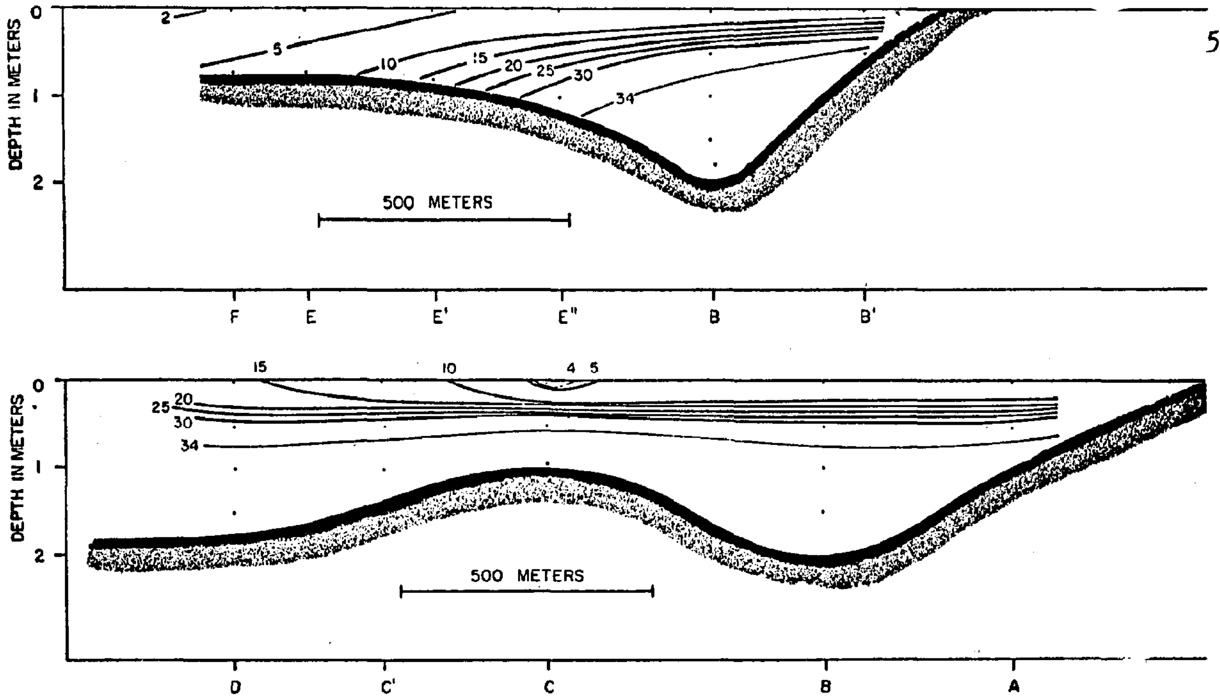
Surface salinity (‰), Falmouth Harbor, Jamaica, 22 January 1961.

Fig. 13. Surface salinity in Oyster Bay after two days' rain (From Taylor et al, 1966).



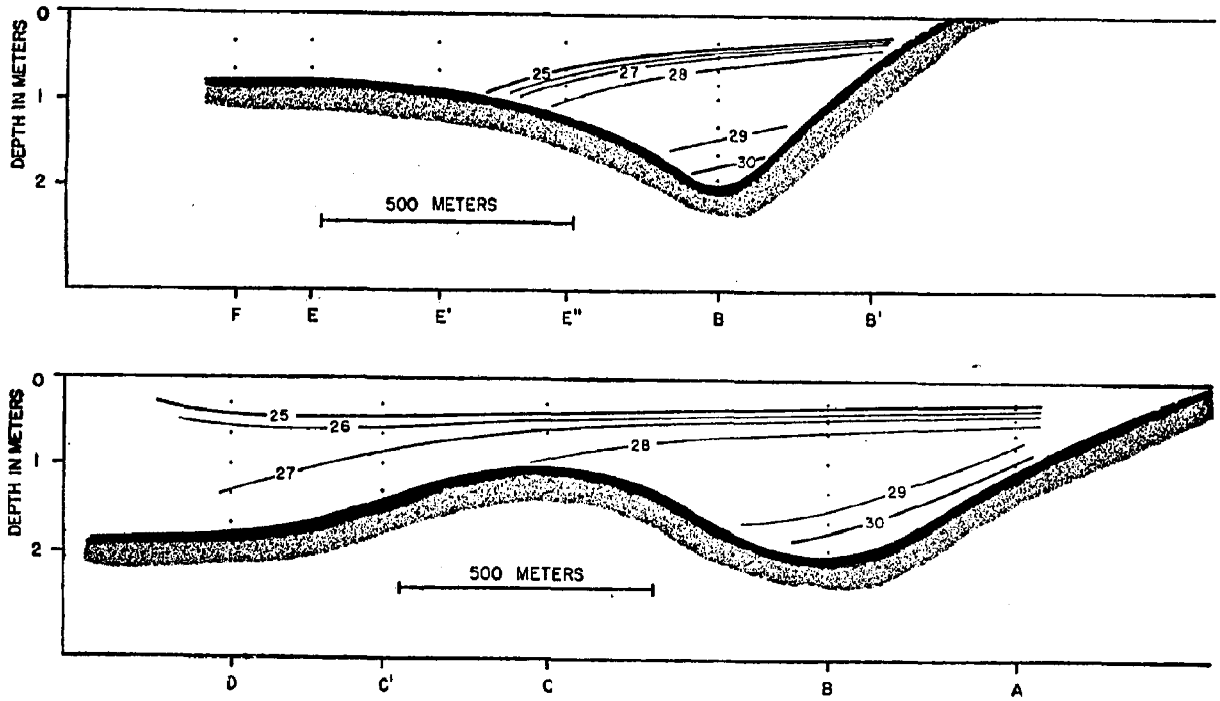
Vertical distribution of salinity (open circles) and temperature (solid circles) at St. B, Falmouth Harbor, Jamaica, showing homogeneity on 19 January 1961 (broken line) and stratification on 22 January 1961 (solid line).

Fig. 14. Vertical distribution of salinity and temperature in Oyster Bay both before and after a rain. See Fig.12 for location of Station B (From Taylor et al, 1966).



Salinity distribution (°/oo), Oyster Bay, Falmouth Harbor, Jamaica, 22 January 1961; top: a section from mouth of Martha Brae River to north shore; bottom: a section from open harbor to head of bay.

Fig. 15. Cross sections showing salinity distribution in Oyster Bay after a rain (From Taylor et al 1966).



Temperature distribution (°C), Oyster Bay, Falmouth Harbor, Jamaica, 22 January 1961; top: a section from mouth of Martha Brae River to north shore; bottom: a section from open harbor to head of bay.

Fig. 16. Cross sections showing temperature distribution in Oyster Bay after a rain (From Taylor et al 1966).

Table 6. Plankton in Oyster Bay when no fresh water layer was lying on the surface. Location of Station B is shown in Fig. 6 (From Taylor et al 1966).

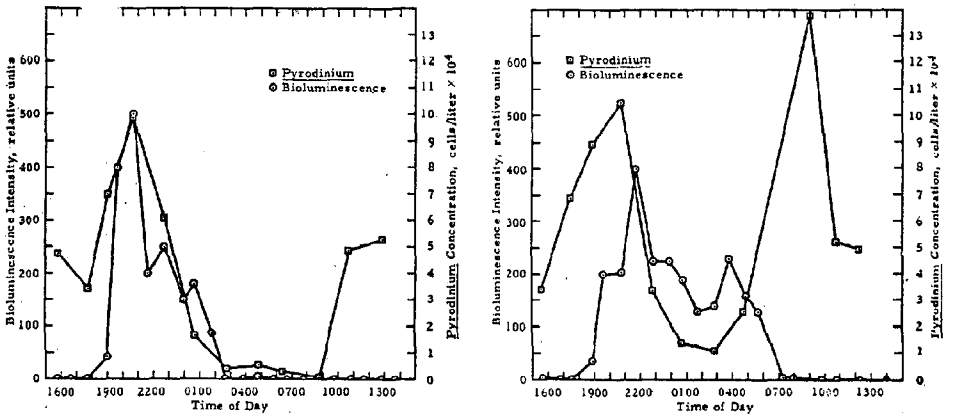
Dinoflagellates and diatoms in plankton at St. B, Oyster Bay, Falmouth Harbor, Jamaica, W. I., 19 January 1961. Cells/liter.

	1800		2115		2230	
	Surface	1 Meter	Surface	1 Meter	Surface	1 Meter
Dinoflagellates						
Prorocentrum micans	–	1,100	–	600	–	500
Dinophysis caudata	600	2,800	7,200	11,000	14,000	5,600
Pyrodinium bahamense	102,000	156,000	219,000	134,000	190,000	129,000
Peridinium breve	–	1,800	2,400	1,700	4,400	1,100
Peridinium divergens	1,800	2,200	7,200	4,400	8,900	1,700
Ceratium hircus	2,900	6,700	6,700	8,300	11,000	3,300
Ceratium fusus	–	–	6,700	600	5,600	–
Ceratium sp.	–	1,100	–	–	1,100	–
Diatoms						
Gyrosigma (*Pleurosigma?*) sp.	600	–	–	–	–	–
Nitzschia closterium	–	–	600	–	–	500
Nitzschia sp.	600	–	–	1,100	–	1,100
Unident. small centrales	14,000	10,000	12,000	14,000	22,000	11,000

Table 7. Plankton in Oyster Bay after a rain. Station locations are shown in Fig. 12 (From Taylor et al 1966).

Dinoflagellates and diatoms in plankton at Sts. B, D, and F in Falmouth Harbor , 22 January 1961. Cells/liter.

	Station B						Station D		Station F
	0900		1230		1500		1100		1130
	Surface	1 Meter	Surface	1 Meter	Surface	1 Meter	Surface	1 Meter	Surface
Dinoflagellates									
Dinophysis caudata	3,300	6,700	1,200	7,400	3,300	5,800	2,200	37,000	1,100
Pyrodinium bahamense	17,000	128,000	24,000	156,000	45,000	148,000	4,400	102,000	–
Peridinium breve	3,300	1,100	600	2,500	1,100	1,200	1,100	3,400	–
Peridinium divergens	–	8,900	2,400	7,400	3,300	8,600	1,100	2,300	–
Ceratium hircus	1,700	5,600	1,200	7,400	2,200	4,600	4,400	26,000	–
Ceratium fusus	–	–	–	–	–	–	–	2,300	–
Unidentified flagellate	–	–	–	–	–	–	–	–	2,200
Diatoms									
Melosira sp.	–	–	–	–	–	–	–	2,300	–
Rhizosolenia sp.	–	–	–	–	–	–	–	–	1,100
Lycomophora sp.	–	–	–	–	–	–	–	–	3,300
Navicula sp.	–	–	4,600	7,400	3,300	1,800	–	–	54,000
Gyrosigma (*Pleurosigma?*) sp.	–	–	–	–	–	–	–	–	3,300
Nitzschia closterium	1,700	–	1,200	5,000	2,200	1,200	1,100	1,200	12,000
Nitzschia sp.	8,300	–	2,400	10,000	5,500	1,200	1,100	3,500	17,100
Unident. small centrales	608,000	–	52,000	18,000	96,000	1,200	–	3,500	–
Unident. small pennales	–	–	600	–	–	–	–	–	13,000



Variations in bioluminescence intensity and number of *Pyrodinium bahamense* cells at 30-cm depth, with time of day, at Oyster Bay, Jamaica, West Indies (March 1965).

Variations in bioluminescence intensity and number of *Pyrodinium bahamense* cells at 90-cm depth, with time of day at Oyster Bay, Jamaica, West Indies (March 1965).

Fig. 17. Variations in bioluminescence intensity and cell numbers with time of day in Oyster Bay (From Soli 1966).

Table 8. Carbon assimilation and chlorophyll a in waters of southwestern Puerto Rico (From Burkholder et al 1967).

CARBON FIXATION AT 31,000 LUX, CHLOROPHYLL *a*, AND ASSIMILATION NUMBERS (A/B) FOR SOME NERITIC BLOOMS OF PHYTOPLANKTON IN SOUTHERN PUERTO RICO

Organism	Date[1]	Location	Chlorophyll *a* A	 B	 A/B
			(mg C m^{-3} hr^{-1})	(mg m^{-3})	
Goniodoma	Feb. 18	W. Magueyes	414	—	—
"	" 28	W. "	380	166.0	2.3
"	" 28	E. "	289	142.0	2.0
"	" 28	W. " (Sunlight)	177	48.1	3.7
Peridinium	Apr. 23	Guayacán	900	69.0	13.0
"	May 1	"	50	8.0	6.2
"	" 1	"	63	10.0	6.3
"	" 2	"	114	28.0	4.1
"	" 2	"	84	21.0	4.0
"	July 9	"	440	79.0	5.6
"	Apr. 29	Offshore	4	0.4	10.0
"	May 1	"	7	1.1	6.4
"	July 12	"	5	0.6	8.3
Dinoflagellates	Feb. 23	Phosphorescent Bay	31	4.4	7.0
"	Apr. 23	"	43	4.4	9.8
"	July 10	"	29	4.0	7.5
"	" 19	"	62	5.4	11.5
Cochlodinium	" 10	"	182	37.0	5.0
"	" 19	"	77	7.0	11.0
Ciliates	Apr. 24	Anemone, La Gata	290	208	1.4
Diatoms etc.	Apr. 29	Guayacán	220	60.0	3.7
Dunaliella	July 10	Salina Fortuna	—	56.0	—
Ciliates	Feb. 26	Briareum, La Gata	60	60.0	1.0
Green flagellates	May 19	Salina Parguera	—	337	—

[1] All dates 1963 except July which is 1964.

ature variations at Magueyes Island of 26.7 - 32.2°C. Burkholder and Burkholder (1958) observed a February temperature of 25.1 and a July temperature of 28.1 at a station just outside Bahía Fosforescênte. Rainfall in the whole region is low, about 30 inches annually; and evaporation is high. Surface water flows from offshore in the direction of increasing salinity in the upper bays (Fig. 1). Margalef considered that steep vertical isohalines (Fig. 20) are indicative of a stronger flow than are the almost horizontal isohalines sometimes observed (Fig. 3). The general current in the region flows from east to west. Margalef (1961b,1962) also viewed the hydrography and plankton distribution in the whole region as being in a quasi steady state, at least in the summer. He regarded the successive types of plankton communities in a transect proceeding from offshore to the small bays as the stages in an ecological succession (Fig. 1), with the bioluminescent bays representing the climax type.

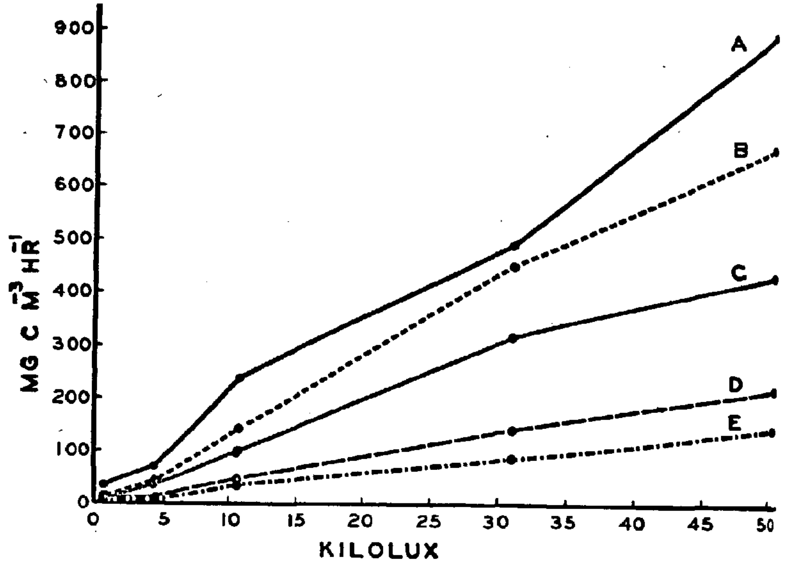
Light penetration in other inshore areas is greater than in the bioluminescent bays; Burkholder and Burkholder (1958) reported that the Secchi disc disappeared at approximately 5.5 m in July at their station just outside Bahia Fosforescente. Dry weights of suspended solids ranged from 1.3 to 3.6 mg/l (Table 5). Vitamin B_{12} in suspended solids ranged from 833 to 1875 mγ per gram (Table 1).

Phytoplankton in the waters coming from offshore contains many pelagic forms (Fig. 1). Blooms of various species occur very commonly but at irregular intervals in the inshore waters. Burkholder et al. studied ^{14}C productivity in blooms of flagellates, ciliates, and diatoms in protected areas of brown water and reported photosynthetic activity at 51,000 lux ranging up to 900 mg C/m^3/hr (Figs. 9 and 18). This was in contrast to offshore blue waters with productivities of 4-7 mg C/m^3/hr^1. Chlorophyll a values ranged from 8 to 208 mg/m^3 in the brown waters and 0.4 - 1.1 mg/m^3 offshore (Table 8, Fig.21). Samples of Goniodoma and Peridinium blooms showed increasing C assimilation with increasing light intensities, even up to the full-sunlight intensity of 130,000 lux (Fig. 19). There was thus no inhibition of photosynthesis at higher intensities.

According to Coker and González (1960) the zooplankton has a greater diversity in nearby waters than in Bahía Fosforescênte itself, and conditions are perhaps more favorable for zooplankton in these other waters. There is also less dominance by copepods here. Tables 3 and 9 show relative abundance of zooplankton species at inshore localities.

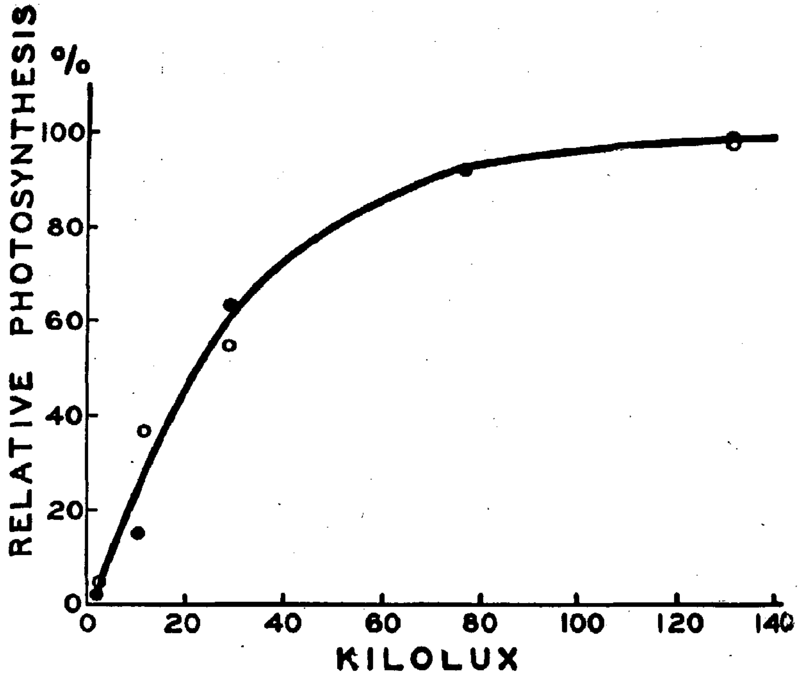
Other Inshore Areas

Other areas which might be classified as having tropical inshore plankton communities have been very poorly studied. Eastern Whitewater Bay and adjacent Coot Bay in Florida's Everglades form a body of water which is not bioluminescent but which appears to be similar to the Puerto Rican bays in certain respects. According to a reference by Tabb and Yokel (1968), there is apparently a single water mass which is stable on a day-to-day basis and has a restricted mixing with adjacent waters. The seasonal salinity program may have values ranging from 5 to 30 ppt, depending upon fresh water inflow from the Everglades.



Carbon assimilation by diverse blooms of microplankton in th neritic waters near La Parguera, Puerto Rico.—A, *Peridinium* sp. bloom a Guayacán, Apr. 23, 1963.—B, *Peridinium* sp. bloom at Guayacán, May 1 1963.—C, *Peridinium* sp. bloom at Guayacán, July 9, 1964.—D, Diatom dinoflagellates and *Chlamydomonas* sp. in Guayacán Channel, Apr. 29, 196 —E, Euglenoids and dinoflagellates at Guayacán, Apr. 22, 1963.

Fig. 18. Carbon assimilation by microplankton in the waters of the southwestern coast of Puerto Rico (From Burkholder et al 1967).



Relative carbon assimilation by *Goniodoma* sp. (solid circles) a the fish pen, Magueyes Island, Feb. 28, 1963, and *Peridinium* sp. (open circles at Guayacán, May 6, 1963, in relation to increasing intensity of natural dayligh in southern Puerto Rico. The maximum values observed (at the highest inte sity) in each experiment are taken as 100 per cent, and the other values ar expressed as a percentage of these maxima.

Fig. 19. Relative carbon assimilation in relation to natural daylight intensity in the waters of the southwestern coast of Puerto Rico (From Burkholder et al 1967).

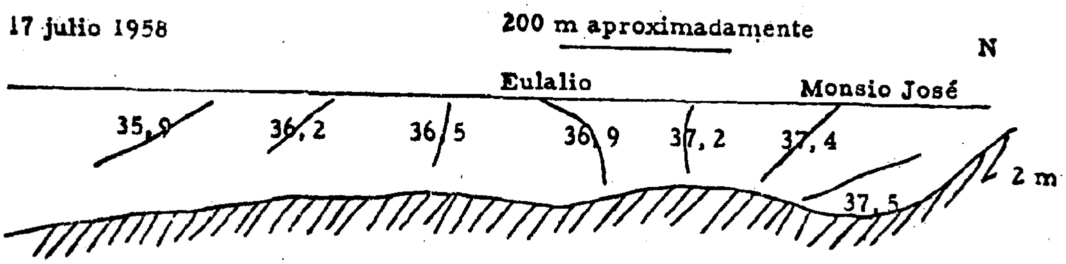


Fig. 20. Isohalines in a cross section of the waters of southwestern Puerto Rico. See Fig. 2 for location (From Margalef 1962; p. 389).

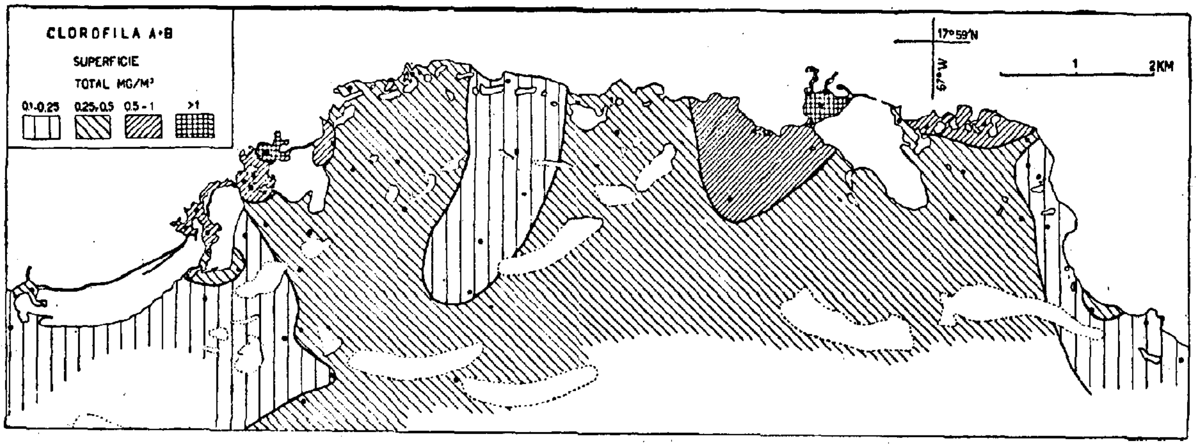


Fig. 21. Distribution of chlorophylls a and b in the waters of the southwestern coast of Puerto Rico (From Margalef 1961b).

Table 9. Copepods in Bahía Fosforescente (From Coker and González 1960).

Mature copepods occurring at any station in as much as one-fourth of the collections or making as much as 0.5% of total copepods, giving, for each station, number of colections in which found (maximum is 24); mean percentage to nearest 0.1; standard error of the mean; and rank in percentage; "*x*" signifies: observed in collection, but not appearing in count.*

	Fosforescente				Montalva				Offshore			
	No. of Col.	Mean %	S.E.		No. of Col.	Mean %	S.E.		No. of Col.	Mean %	S.E.	
Oithona minuta	24	20.7	2.34	1	24	10.6	2.29	3	24	6.0	1.01	4
Acartia tonsa	24	17.2	3.00	2	19	2.3	0.88	6	7	0.2	0.86	12
Paracalanus crassirostris	24	11.4	2.80	3	24	21.7	4.45	1	24	27.5	4.13	1
Oithona simplex	21	7.7	2.57	4	24	12.3	2.32	2	24	14.5	2.73	2
Euterpina acutifrons	18	0.9	0.28	5	18	2.5	1.00	5	22	2.0	0.49	6
Acartia spinata	6	0.2	0.17	6	21	2.7	1.32	4	15	1.3	0.60	7
Oithona nana	5	0.2	0.09	7	18	1.9	0.82	7	13	3.0	0.86	5
Paracalanus parvus	6	0.1	0.13	8	16	1.1	0.49	8	24	7.8	2.56	3
Acartia lilljeborgi	6	0.1	0.05	9	9	0.2	0.10	10	10	0.4	0.16	11
Corycacus amazonicus	3			10	7	0.2	0.09	11	18	0.8	0.17	9
Corycaeus americanus	0				7	0.1	0.04	12	18	0.9	0.29	8
Temora turbinata	1				10	0.3	0.11	9	16	0.5	0.11	10
Centropages furcatus	0	*x*			1				8	0.1	0.05	13

* Immature copepods made 41.4% of copepods for Fosforescente, 43.8% for Montalva, 34.8% for Offshore.

However, there is no sudden runoff from adjacent areas, and tidal exchange is minimal. The average depth is slightly more than a meter. The open waters of the bay grade into broad mangrove areas in the upper reaches. There is apparently an indigenous phytoplankton community dominated by small-celled diatoms, although species determinations and their relative abundances have not been published. Further information about Whitewater Bay would be useful in giving it a designation in the estuarine classification system.

Even less is known about most other bodies of water in southern Florida, and it is not clear whether they should be classified as having tropical inshore plankton communities. Davis and Williams (1950) did a survey of the plankton of mangrove areas in southern and western Florida. They considered these areas as being subject to strong seasonal patterns, though there was no seasonal study made of the plankton. They regarded most or all of these estuaries as well flushed by the tides; this would inhibit the development of an indigenous planktonic community in a given body of water. Salinities were extremely variable from one area to the next and were undoubtedly strongly influenced by fresh water runoff through the Everglades. There was a marked absence of dinoflagellates from the phytoplankton and of coelenterates, platyhelminths, and chaetognaths from the zooplankton. Much more research needs to be done on the plankton in these waters and on the possible seasonal cycles before borderline cases here can be resolved to fit into the classification. There may well be other communities in areas of Florida and Hawaii which should be classified as tropical inshore plankton types.

DISTURBANCE

Because of their intricate balance of physical, chemical, and biological factors the bioluminsecent bays appear to be particularly susceptible to man-made disturbances. One of the most important considerations is that these ecosystems are apparently adapted to low water exchange with the open sea. The bioluminescence of a bay on New Providence Island, Bahamas, was completely and immediately destroyed when its channel to the sea was widened and deepened to make it more accessible for small boats. The bioluminescence of Bahía Monsio José is reported to have declined markedly since a small canal was dug connecting it to the sea and opening up another channel for water exchange. It seems clear that further alterations of this type must not be made if bioluminescent bays are to be preserved.

Since the bioluminescence is dependent on a single species, Pyrodinium bahamense, the balance in these bays is particularly delicate. The exact ecological niche of this species is not known. Small changes in the quality or quantity of input from surrounding areas could easily favor some other species and cause the bioluminescence to be lost. Hence, it is necessary to consider the maintenance of the watersheds and mangrove fringes around the bays as well as the bays themselves. Qualitative changes in the input through the mouths could also have a marked effect in the long run.

Because of their slow flushing rates these bays could act as traps for substances which might lead to an alteration of the natural communities. Of course, Oyster Bay in **Jamaica** is currently receiving a certain amount of input from sugar and banana plantations through the Martha Brae River; but the exact nature of this input has not been evaluated. Nevertheless, this suggests that the ecosystem in bioluminescent bays might handle some agricultural runoff without permanent alteration.

Domestic sewage and petrochemical wastes are already facts of life along Puerto Rico's southwestern coast, and it appears that these stresses are about to mushroom. Prevailing currents in the region are such that the entire inshore area will be subjected to these wastes. It cannot be expected that the inshore tropical plankton communities will receive this stress without being altered, perhaps irreversibly. More research is needed.

Chapter B-5

TROPICAL BLUE-WATER COASTS

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Where the deep blue oceans of the tropics approach populated continents they are usually protected from a sudden encounter with land by broad stretches of gently shoaling green water. In a few areas and under special circumstances, however, the green water zone is missing or greatly reduced. The result is what we will call a blue-water coast where a water mass with essentially open ocean conditions and communities intrudes to within a very short distance of the shore. Such regions may not be classified as estuarine in the sense that full oceanic salinities prevail.

The great majority of blue-water coasts occur where oceanic islands such as Puerto Rico and Hawaii rise suddenly in the midst of tropical oceans. Here the conditions are almost totally oceanic and the meager runoff of water, nutrients and sediments from the steeply rising islands does not greatly alter the characteristics of the surrounding oceans.

Continental coastal regions, on the other hand, are characterized by extensive drainage systems carrying great loads of sediments and nutrients which build sedimentary estuaries and broad expanses of coastal green-water overlying gently sloping continental shelves. In only one area of the continental United States is there a true tropical blue-water coast where the land falls away quickly into the sea; this is along the southeast coast of Florida. Here the Florida Current flows within a few kilometers of the shore at a speed of two or three knots. Because oceanic conditions are continually and forcibly thrust upon this coastal environment by the Florida Current, there is no opportunity for the continental runoff to establish much of a green-water zone, and consequently, blue-water conditions may reach to within three kilometers of the beach. On the southwest coast of Florida where there is no great current and the continental shelf slopes very gradually, the true blue-water zone lies over one hundred kilometers offshore.

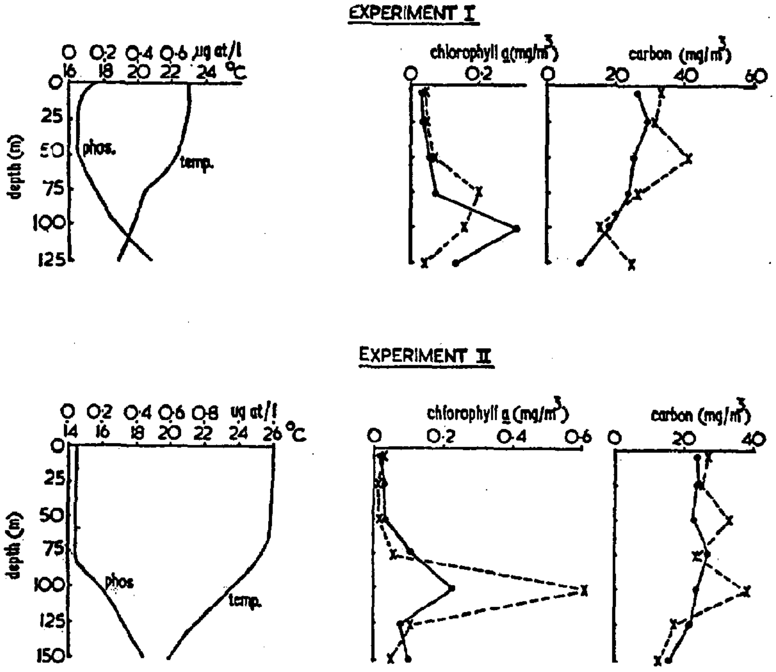
In comparing the blue-water coasts of Puerto Rico, Hawaii and southeast Florida certain general characteristics emerge, both physical and biological, which appear to be common to all three regions. These characteristics are basically those of the tropical open oceans themselves and have been only slightly modified by the proximity of land.

PHYSICAL CHARACTERISTICS OF THE SYSTEM

Tropical oceans and blue-water coasts are distinguished by extremely clear, transparent water which because of its low levels of phytoplankton, suspended and dissolved substances shows a deep cobalt blue color. This transparency allows a much deeper penetration of incident surface radiation than occurs in turbid inshore waters or oceanic water at higher latitudes (Fig. 1b). The result is an euphotic zone which may extend well below 100 meters in contrast to green coastal waters where it is usually no deeper than 30 to 40 meters.

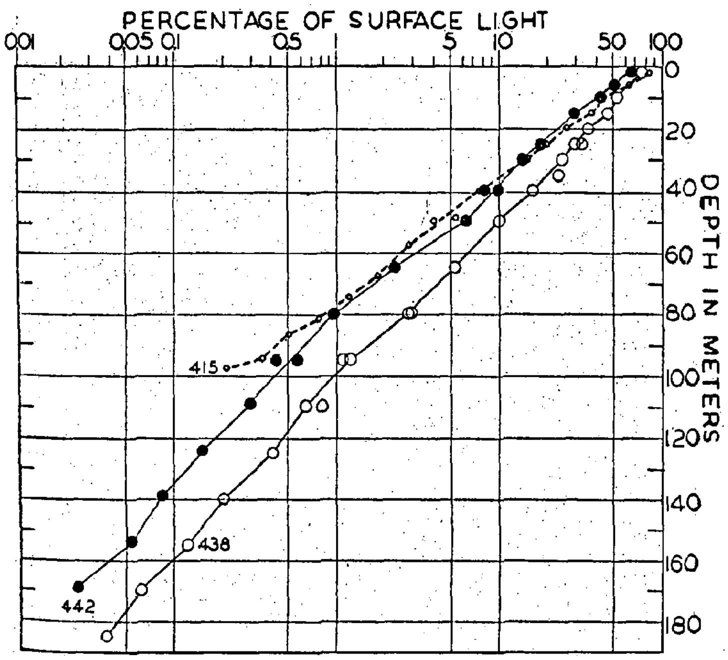
Because the solar radiation remains more or less constant throughout the year in the tropics, the temperature of the surface waters shows little fluctuation. In the Florida Straits the annual variation of the surface 100 meters is only about 4° C (Fig. 2). This stable input of solar energy creates a remarkably deep isothermal layer overlying a permanent thermocline. Since there is no seasonal "pulse" or temperature change, the thermocline is rarely destroyed and its depth depends upon the amount and duration of surface winds. Off the Hawaiian Islands this permanent thermocline is ordinarily found at a depth of 200-300 meters, but on the protected Waianae coast of Oahu, where the strength of the prevailing trade winds is reduced, the thermocline is found at 70-100 meters (Brock and Chamberlain, 1968).

The permanency of the tropical thermocline serves effectively to prevent vertical mixing between the warm surface layer and the deep cooler waters. For this reason there can be little seasonal recharging of nutrients in the surface water as occurs at higher latitudes. As a result tropical surface waters are characterized by extremely low standing stocks of nutrients (Fig. 2). Greater concentrations of nutrients are found where upwelling occurs as in the equatorial Pacific or where the thermocline rises near the surface as in the eastern tropical Pacific. Vertical patterns in blue water of the Gulf of Mexico are shown in Fig. 1a.



Vertical distributions of temperature, phosphate, chlorophyll *a*, and carbon for C^{14} experiments. I (24°57′N, 84°08′W; 24-IV-62), II (24°53′N, 84°39′W; 25-IV-62). For chlorophyll *a* and carbon: solid line, 1200 hours; dashed line, 0000 hours.

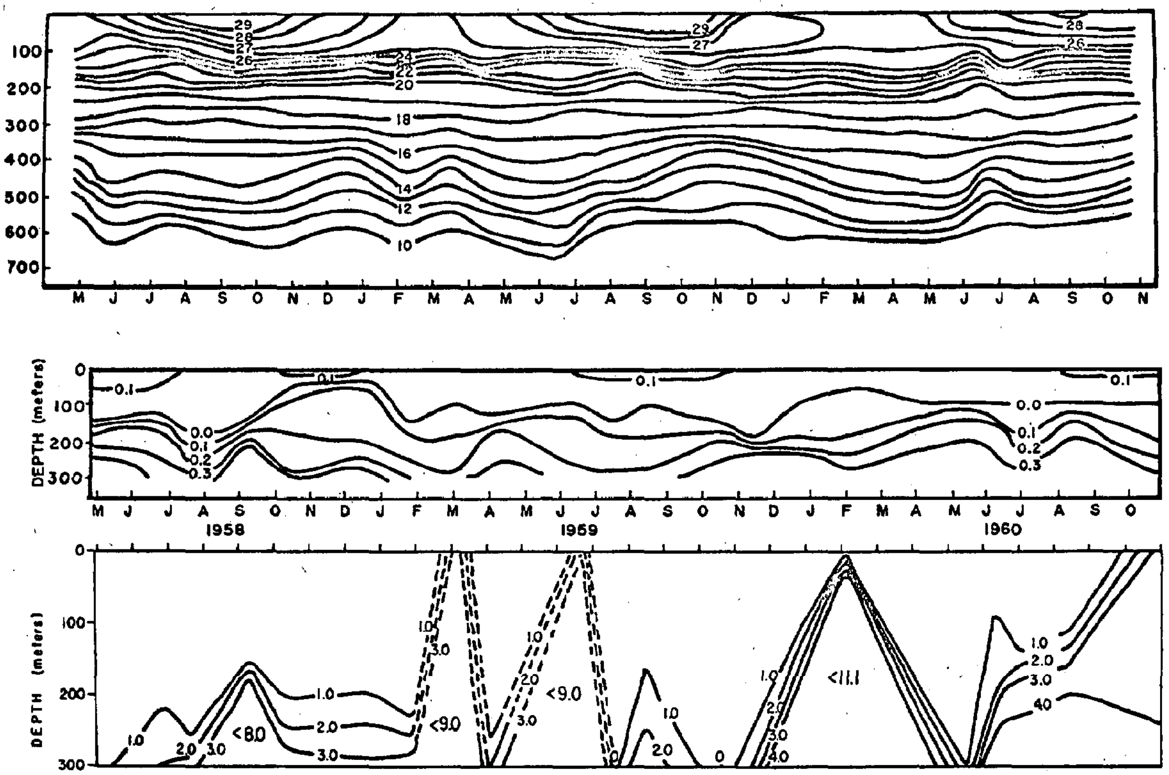
Fig. 1a. Vertical patterns in the Gulf of Mexico (Steele, 1964).



Relation between depth and irradiation expressed as a percentage of the light just over the surface.

Series	Locality	Latitude	Longitude	Date	Time	Sky	Sea	Wind
415	Gulf Stream (S of Grand Banks)	39°56′N	48°40′W	Sept. 15, 1935	15:35–17:00 (L.A.T.)	o	slight	3–4
438	Cayman Sea	18°38′	79°12′	Feb. 28, 1937	10:45–12:42 (E.S.T.)	bc	smooth	1
442	Gulf of Mexico	29°14′	87°48.5′	April 11, 1937	10:30–11:18 (C.S.T.)	b	smooth	1

Fig. 1b. Penetration of incident surface radiation (From Clarke 1938).



Vertical and seasonal distributions, 1958 through 1960, of: *top*, temperature; *middle*, phosphate-phosphorus in the upper 300 m: *bottom*, nitrite-nitrate nitrogen in the upper 300 m.

Fig. 2. Distribution of temperature, phosphate-phosphorus, and nitrite-nitrate-nitrogen according to season and water depth in the Florida Straits (From Corcoran and Alexander 1963).

STRUCTURE OF THE BIOLOGICAL COMMUNITY

Since the communities of phytoplankton and animals associated with surface waters of blue-water coasts are typically pelagic, it is not surprising to find a great deal of similarity whether they be from the Hawaiian Islands or the southeast coast of Florida. This is especially noticeable with the mobile species at the higher trophic levels.

Perhaps, the most conspicuous feature of tropical blue-water communities is the great number of species present as compared with waters at higher latitudes. This phenomenon of higher numbers of species at lower latitudes holds for the dinoflagellates, foraminifera (see Fig. 3) and pelagic fishes, but does not apply to the diatoms which flourish in cold polar regions (Wood, 1965). Table 1 shows the number of holoplanktonic animals from six types of oceanic systems; clearly the tropical blue-waters far exceed any other water mass in numbers of species. Evolution seems to have favored greater numbers of species with less individuals rather than larger populations within species (Klopfer and MacArthur, 1960, 1961). Whether this contributes to, or is a result of, the relatively stable environmental conditions can only be guessed at.

The Primary Producers

Characteristically many of the animals of the communities which lie below the surface waters make extensive diurnal vertical migrations. These movements serve to remove energy from surface waters to the depths much more quickly than if energy transfer depended upon sinking rates alone. Movements of herbivores into surface waters at night can be correlated both with a sharp decline in phytoplankton numbers (Wood and Corcoran, 1966) and a shift of the vertical maxima of phytoplankton (Fig. 4.).

Phytoplankton of the tropical oceanic waters are dominated by very small algae called nannoplankton. Table 2 shows the increase of the relative importance of nannoplankton over net plankton at lower latitutes. Miller and Moore (1953) found that the nannoplankton biomass of the Florida Straits is up to 1000 times that of the net phytoplankton such as larger diatoms and armored dinoflagellates.

Typically the nannoplankton include the Chrysomonad and Cryptomonad flagellates, small naked dinoflagellates and small diatoms. The Chrysomonads (cocolithophorea and golden brown flagellates) dominate in many tropical regions (Allen, 1967). The nannoplankton were overlooked in early considerations of standing crops of tropical waters because they were not retained by standard plankton nets. It has recently become apparent that they are capable of very rapid turnover, and accelerated primary production (Odum, Beyers and Armstrong, 1963).

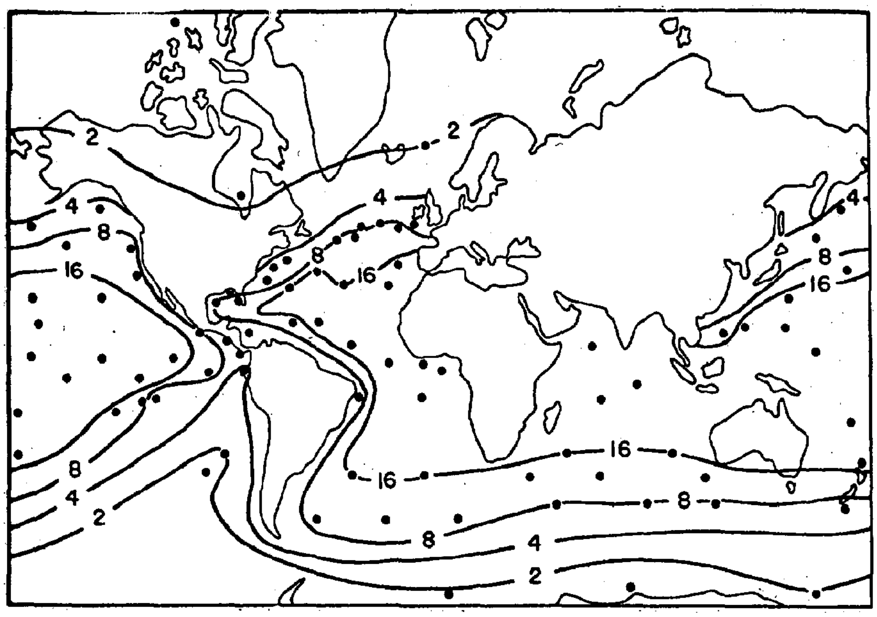
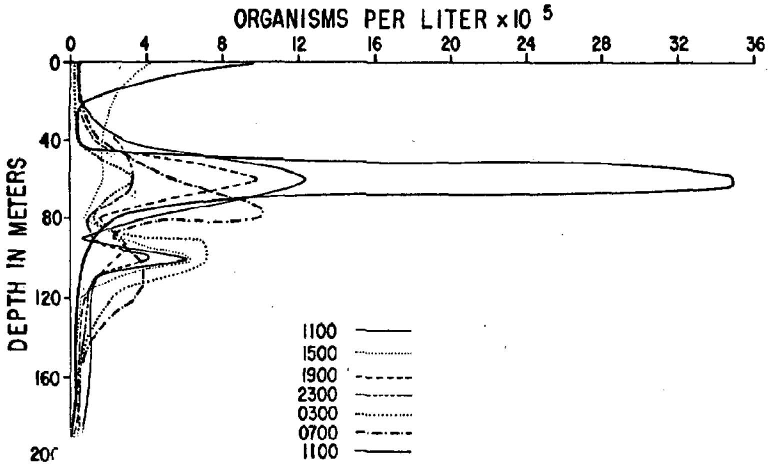


Fig. 3. Contoured numbers for recent species of planktonic foraminifera. Equatorial centering of the species gradient is clear, as is the major source of noise introduced by ocean current transport of these planktonic organisms (From Stehli 1968).



Distribution of phytoplankton with depth over 24 hours in the Tongue of the Ocean.

Fig. 4. Phytoplankton distribution according to water depth (From Wood and Corcoran 1966).

Table 1. Numbers of species of holoplanktonic animals in world oceans (From Russell 1935).

Location	Number of Species
Warm oceans	1378
Arctic and arctic boreal oceans	58
Antarctic and subantarctic oceans	90
Deep sea	340
Cosmopolitan	15
Total	1881

Table 2. Comparison of phytoplankton biomass caught in different regions of the oceans (From Yentsch and Ryther 1959).

The percentage of phytoplankton biomass caught by a No. 25 plankton net in different regions of the oceans

Location	Latitude	% of the total	Author
Scoresby Sound, East Greenland .	70°N	66	Digby (1953)
Off Plymouth, England..........	50°N	10–26	Harvey (1950)
Long Island Sound	41°N	9–56	Riley (1941)
Vineyard Sound	41°N	2–47	
New South Wales, Australia	33°S	3–4	Wood and Davis (1956)
Tortugas	24°N	1	Riley (1939)

Table 3. Volume of net-caught zooplankton from the eastern tropical Pacific (From Mais and Jow 1960).

Organism	Fraction by volume	Fraction by number
Copepods	20%	63%
Tunicates	15%	6%
Chaetognaths	12%	15%
Siphonophores	8%	1%
Euphausids	5%	5%
Medusae	3%	1%
Decapods	2%	1%
Amphipods	1%	1%
Ostracods	1%	1%

The Decomposers

In contrast to the situation in some shallow estuaries, the decomposers (fungi and bacteria) do not play a significant rôle in the blue-water coastal community. Although very little quantitative data exist concerning their presence and importance, the general impression is that their standing crops are exceedingly low (Wood, 1965) and that they are not important in the mineralization and recycling of nutrients (Johannes, 1968).

The Consumers

Little quantitative data exist concerning either planktonic or nektonic consumers of tropical seas. There are, however, fairly complete faunal lists for many regions. Those for the Florida Current are: Moore (1952) for the euphausids, Moore (1953) for the siphonophores, Owre (1960) for the chaetognaths, Owre (1962) for the copepods, Voss (1956) for the cephalopods, Wormelle (1962) for the pteropods, Steiger (1969) for the benthic fishes and Devaney (1969) for the midwater fishes.

The most important herbivores of blue-water coasts are the copepods. In the Florida Current they constitute at least one third of the animal biomass taken in a plankton net (Bsharah, 1957) and are of even greater importance numerically. Their importance in the eastern tropical Pacific is shown in

Table 4. Comparison of phosphorus cycling in inshore waters and offshore blue waters (From Pomeroy 1961)

Item	Concentration mg atoms/m^3	Turnover rate mg atoms/m^3/ hr	Residence time hrs
Surface coastal water off Georgia, 31 N. Lat.	0.1 - 0.8	0.1 - 0.4	34 - 155
Gulf stream surface water off Georgia	0.1	0.8	4

Table 3. Another group which are predominantly herbivorous are the euphausids, although they are not as numerous in the tropical surface waters as in the Antarctic. On the other hand, pteropods, heteropods and tunicates are far more important in tropical waters than toward the poles.

Major planktonic carnivores include siphonophores, chaetognaths, fish larvae and juvenile cephalopods. The fish larvae of blue-water coasts are especially numerous due to the tendency of many coastal and estuarine fishes to move offshore to spawn. In the surface waters the larger carnivores are represented during the day by pelagic fishes, but at night diurnal mirgrations bring mesopelagic squids and fishes into predominance. As previously mentioned the large pelagic fishes are very similar in all tropical oceans. Sports fishermen off Florida, Puerto Rico and Hawaii all catch yellowfin tuna Thunnus albacores, skipjack tuna Katsuwonus pelamis, dolphin Coryphaena hippurus, wahoo Acanthocybium solandri, amberjack Seriola spp., rainbow runner Elagatis bipinnulatus along with species of sailfish and marlin.

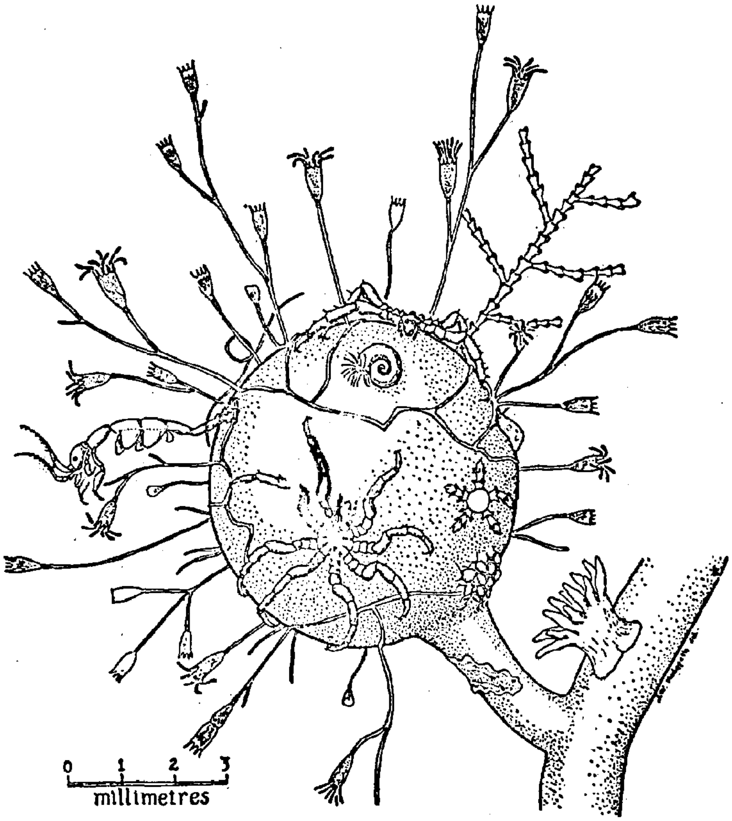
Drifting Subsystems or "Superstrates"

A special subsystem of the blue-water regions are the drifting communities. These are formed when pelagic fishes and other organisms become associated with drifting material such as Sargassum (see Gordon, 1938), Physalia, coconuts, logs, boards, pumice, coconut fronds, slabs of cork, rafts and other flotsam. Commercial and sports fishermen have long realized the value of concentrating their efforts around such objects. Japanese and Indonesian fishermen even construct floating rafts which they anchor and visit again and again for good catches of fish. Miami charterboat fishermen can usually expect to take at least one dolphin underneath a floating piece of wood. Catches of several hundred fish have been recorded from under a single plank.

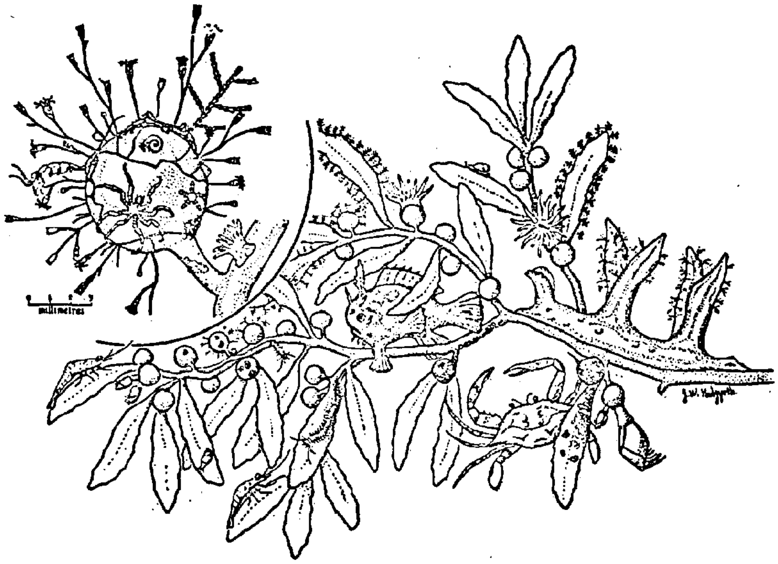
Gooding and Magnuson (1967) present a good review of past work and describe their own experience with a floating raft in the open Pacific. Over a period of many days they observed hundreds of adult and juvenile fishes around the raft including 27 species which were permanent residents. They concluded that floating objects were beneficial to the fish in three ways: (1) they provided portection from predation for smaller fishes, (2) they concentrated the food supply for larger fishes and (3) they served as "cleaning stations" for the removal of parasites from the larger fishes by smaller ones. In conclusion they described floating objects as a relatively rare "superstrate" in an environment notable for its horizontal homogeneity. Such superstrates have the same ecological significance to certain pelagic fishes that a substrate has to inshore fishes. Sargassum associations are shown in Fig. 5.

The Neuston

Another type of superstrate is the air-water interface. Living in close association with this layer are the animals known as neuston (summarized by David, 1965). Included are the only insects which live in the open ocean, the five species of Halobates or water striders, along with a number of organisms which float on the surface (Physalia and Velella) and many more which exist just below the surface film. All of these animals are subject to great stress



The faunal association of a sargassum bladder, Texas coast. The hydroids are *Obelia* and *Sertularia*, the pycnogonid is *Tanystylum orbiculare*. Other forms include the sargassum anemone, *Anemonia sargassensis*, a caprellid, a flatworm, a small tubiculous polychaetes *(Spirorbis)*, a juvenile ophiuran and a small colony of bryozoa. (From Hedgpeth, 1948.)



–Displaced benthos of the Sargassum

The examples illustrated are taken from Sargassum found near shore in the northern Gulf of Mexico, and include *Scyllaea pelagica*, *Portunus sayi*, *Histrio histrio*, *Anemonia sargassensis*, *Platynereis dumerili*, *Litiopa melanostoma*, *Latreutes fucorum*, Bryozoa, serpulid worms, and hydroids. Inset: details of hydroids, a caprellid, the pycnogonid *Tanystylum orbiculare*, a juvenile ophiuran, and a polyclad worm.

Fig. 5. Floating Sargassum association (Hedgepeth, 1948, 1957).

conditions since the physical and chemical conditions of the environment are capable of greater and more rapid changes than occur elsewhere in the open sea. In addition they are exposed to the full spectrum of sunlight.

The neuston are characterized by an intense blue color----quite different from plankton in the water column a few meters below. This blue color which is found in copepods, decapod crustacea, medusae, fish, squid and salps, is probably a form of adaptive coloration affording some concealment in the brilliant blue surface water. This color is due to pigments in some animals and interference effects in others.

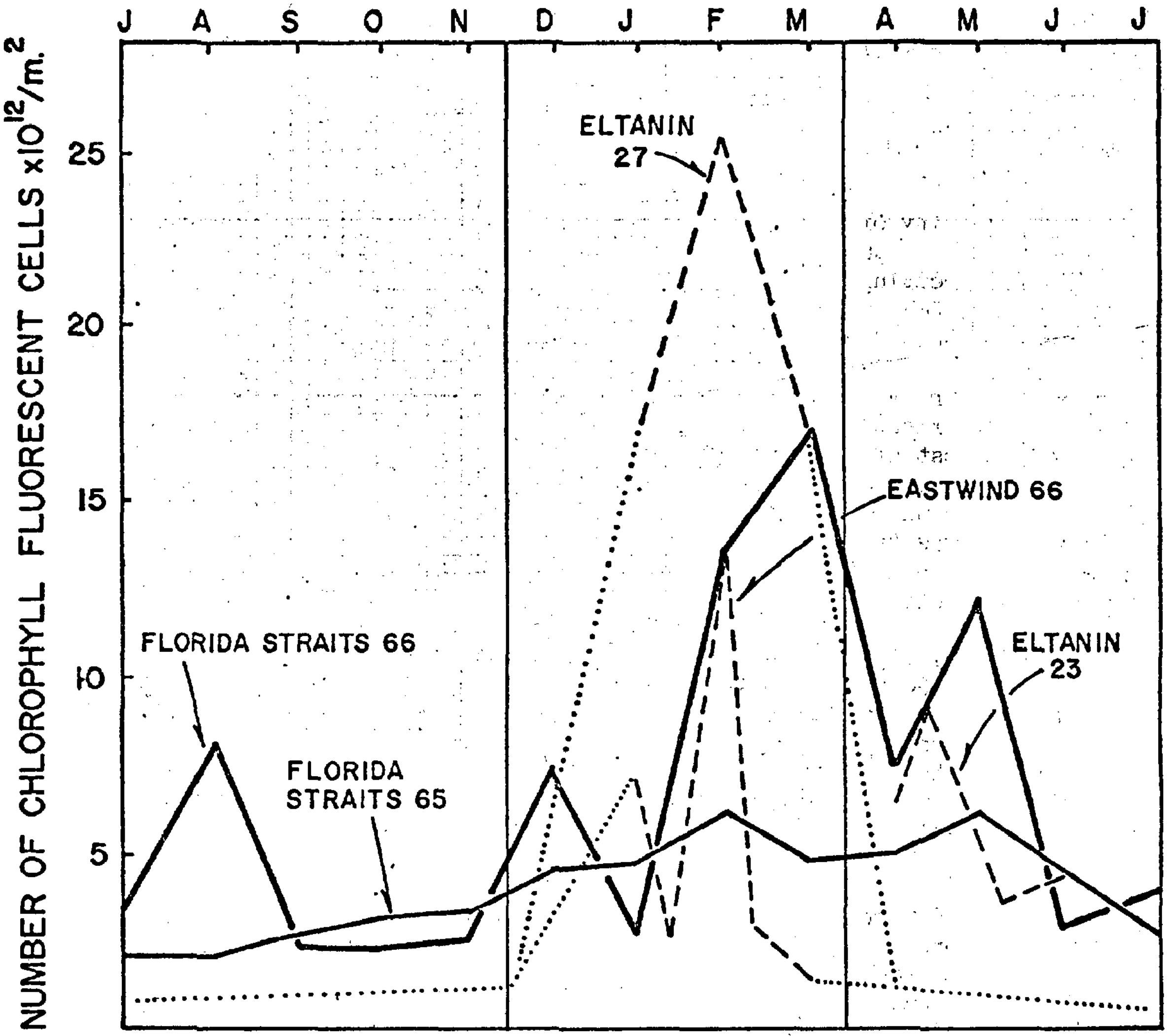
PRIMARY PRODUCTIVITY OF THE SYSTEM

The scarcity of dissolved nutrients in tropical surface waters has been interpreted in the past as an indication that primary production proceeds at low levels creating practically a biological desert (Hensen, 1890; Lohmann 1917; Sverdrup, Johnson, and Fleming, 1942). This concept was further strengthened by observations of generally low standing crops of phytoplankton in the tropics.

More recently it has been pointed out by Pomeroy (1961) that measurements of dissolved nutrients in natural waters give a very poor indication of availability since most of the nutrients at any given moment may exist inside living cells. If these cells are capable of turning over the nutrients at a rapid rate, then there will be a constant supply for other cells which are able to concentrate nutrients from a dilute solution. This, in fact, appears to be the case in tropical seas where the phytoplankton is dominated by small forms with rapid metabolic rates.

Pomeroy (1961) has compared the phosphorus budget for a coastal green-water system off Georgia with the Gulf Stream lying further offshore (Table 4). Although the concentration of phosphorus is much lower in the Gulf Stream than in the coastal water, the turnover rate is higher and the residence time far shorter in the blue-water. One reason for these rapid turnover rates is the ability of many organisms to absorb and utilize nutrients while they are still in an organic form rather than waiting for the slow process of mineralization to an inorganic form.

This rapid turnover of nutrients by organisms coupled with (1) a very deep euphotic zone, which may be three to four times deeper than in green-water, and (2) a constant supply of solar energy through out the year suggests that tropical surface waters may be more productive on a year-round basis than was formerly supposed. Walsh (1969) compared the seasonal variation of Antarctic and Florida Current phytoplankton numbers throughout the respective euphotic zones (Fig.6a) and found the constant low standing crops of the tropics comparable to the wild fluctuations of the Antarctic on an annual basis. As further evidence, yearly production for tropical blue-water and other oceanic areas are presented in Table 5. Such data are not strictly comparable since ^{14}C, light and dark bottle O_2 and nutrient depletion methods of measuring primary production are not standardized. However, the data can be used as a rough approximation of the energy input of these areas. From the table the following



Annual variation of standing crop in the Straits of Florida(solid lines) and the suggested annual variation of areas in the Southern Ocean(dashed are observed and dotted are postulated) .

Fig. 6a. Seasonal variation of Antarctic and Florida Current phytoplankton (From Walsh 1969).

Table 5. Yearly production of various oceanic areas.*

Area	Yearly Rates ($g\ C/m^2/year$)	Type of Production	Source
Tropical Blue Water			
Florida Current	67-182.5	Net-Gross	Corcoran and Alexander (1963)
Sargasso Sea	167	Gross	Riley, Stommel, and Bumpus (1949)
Sargasso Sea	72	Net-Gross	Ryther (1963)
Hawaii	37	Net-Gross	Steemann Nielsen (1954)
Hawaii	123	Gross	Doty and Oguri (1956)
Marshall Islands	182.5	Gross	Sargent and Austin (1954)
Indian Ocean	73-89.3	Net-Gross	Steemann Nielsen and Jensen (1957)
Caribbean	51-70	Net-Gross	Steemann Nielsen and Jensen (1957)
Antarctic			
Bellingshausen Sea	4.8	Net-Gross	Burkholder and Mandelli (1965)
Bellingshausen Sea	28.8	Net-Gross	El-Sayed (1967)
Bransfield Strait	26.8	Net-Gross	Burkholder and Mandelli (1965)
Bransfield Strait	331.2	Net-Gross	El-Sayed (1967)
Weddell Sea	84	Net-Gross	El-Sayed and Mandelli (1965)
Drake Passage	92.4	Net-Gross	El-Sayed (1967)
Marguerite Bay	55.2	Net-Gross	El-Sayed (1967)
Antarctic Ocean	100	Gross	Ryther (1963)
Arctic			
Polar sea	1.0	Net-Gross	Apollonio (1959)
Polar sea	1.0	Net-Gross	English (1959)
Temperate			
Georges Bank	309	Gross	Riley, Stomel, and Bumpus (1942)
Long Island Sound	470	Gross	Riley (1956)
Benguela Current	167-912	Net-Gross	Steemann Nielsen (1954)
Continental slope off New York	100	Gross	Ryther and Yentsch (1958)
Coastal water off New York	160	Gross	Ryther and Yentsch (1958)
North Sea	45-100	Gross	Steele (1958)

*compiled by John Walsh. In many cases annual production was estimated from the original authors' daily production rates.

conclusions can be drawn: (1) tropical blue-water systems may be equivalent to or more productive than polar regions, and (2) temperate systems with seasonal pulse energy and nutrient cycles are more productive than tropical blue-water or single pulse polar systems.

Seasonal Cycles--A Possible Steady State?

Since primary production appears to proceed at a constant low level throughout the year in the tropics, it has been suggested that these blue-water systems approach a steady state situation. Cushing (1959a and b) distinguishes two extreme types of production cycles, one unbalanced with strong seasonal fluctuations as occurs in temperate and cold seas and the other "fully balanced" or in a steady state with no change in standing crops as found in non-upwelling tropical regions. The occurrence of apparent yearly balances between phytoplankton production and zooplankton standing crops in tropical ocean areas has been described by Holmes (1958) for the eastern tropical Pacific, Menzel and Ryther (1960) for the sub-tropical Sargasso Sea and Bsharah (1957) for the Florida Straits.

Blackburn (1966) working in a specific area of the eastern tropical Pacific concluded that standing crops of phytoplankton, herbivores and primary carnivores occurred in ways that were consistent with steady state conditions. He found such conditions lacking for other areas of the eastern tropical Pacific, but did not deny their possible existence. In studying Bsharah's seasonal distribution of total phosphorus in the Florida Straits (Fig. 6b) it appears that a steady state is approached, although some fluctuation is apparent. More data are needed to determine whether these small fluctuations are of significance in the annual operation of the system or merely "noise".

Boundary Effects

As a general rule the standing stocks of both dissolved organic and inorganic compounds and the biomass of organisms increase as blue-water systems approach land (discussed for Hawaii by Doty and Oguri, 1956). The cause for this enrichment can be traced to (1) runoff from land, (2) primary production of inshore coastal systems and (3) coastal upwelling. The enrichment phenomenon becomes more pronounced when the land is continental rather than an oceanic island. With very small islands the effect may be negligible. Fig. 7 shows the characteristics of a blue-water system which approaches a small tropical Pacific Island. It is interesting to note that oceanic conditions remain relatively unchanged to within less than a mile of the shore.

Along continental blue-water coasts the effects may be much greater. Corcoran (1967) has shown for the Florida Current (Figs. 8 and 9) that the concentrations of both soluble iron and copper increase markedly as the Florida coast is approached. Concentrations in the center of the Florida Straits were less than half that of the shallow Fowey Rocks near Miami. The Cay Cay region lying offshore from the Bahama Islands had higher concentrations than the center of the Straits, but were significantly lower than along the Florida coast.

At the inshore boundary of blue-water there is usually a rise in the standing stocks at the higher trophic levels. It is no accident that the world's

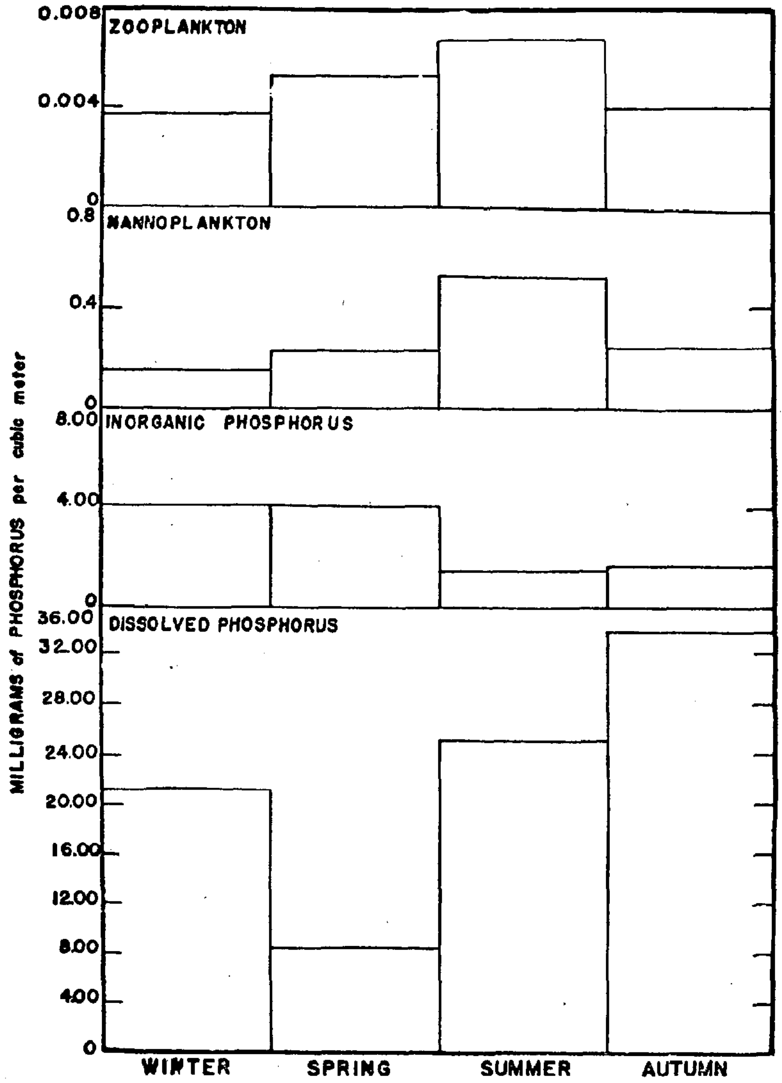
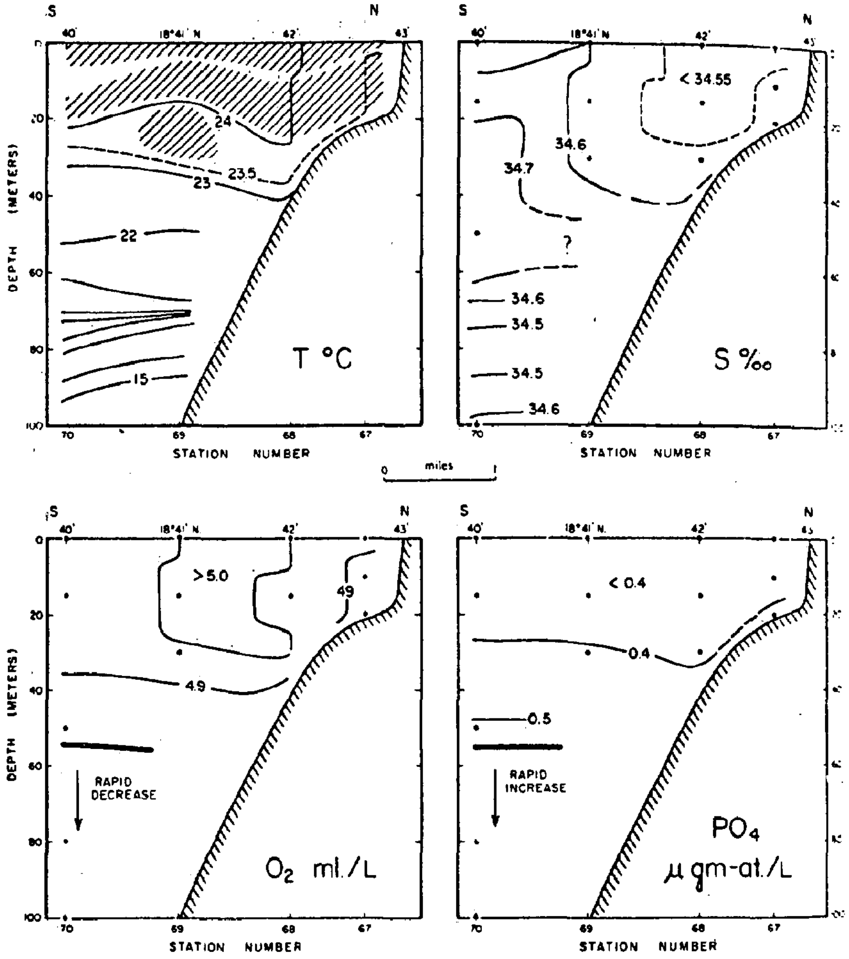


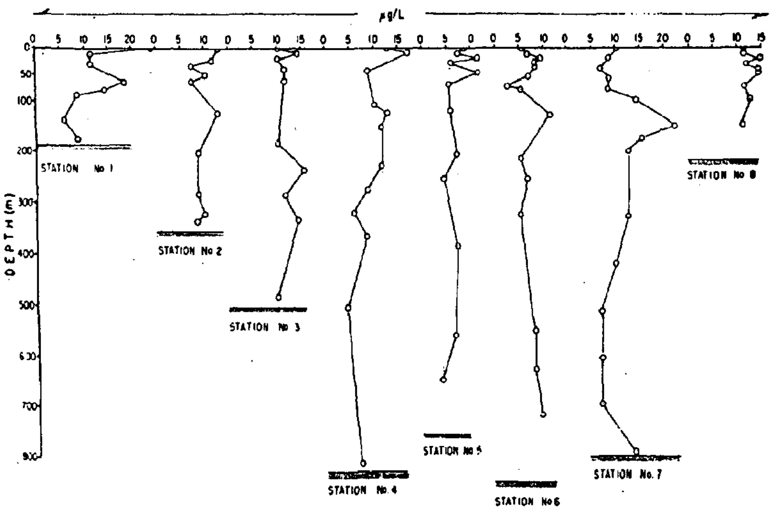
Diagram showing distribution of total phosphorus in euphotic zone at Forty-Mile Station.

Fig. 6b. Seasonal distribution of total phosphorus in the Florida Straits (From Bsharah 1957).



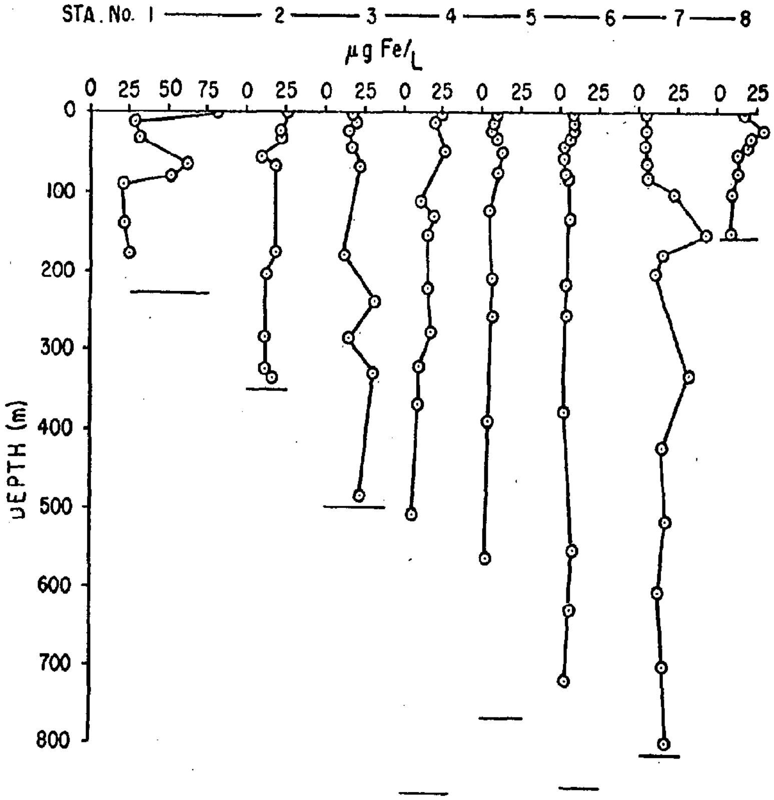
Socorro Island Survey. Distributions of temperature (°C), salinity (°/oo), dissolved oxygen (ml./L.), and inorganic phophate (µ gm-at./L) in the southern section. The shaded areas in the temperature distribution indicate nearly vertically-isothermal water

Fig. 7. Blue water coast characteristics near a small tropical island in the Pacific (From Bennett and Schaefer 1960).



The vertical and horizontal distribution of the total soluble copper between Fowey Rocks and Cat Cay during January 1963.

Fig. 8. Concentration of soluble copper in the Florida Current (From Corcoran 1967).



The vertical and horizontal distribution of the total soluble iron in the Straits of Florida between Fowey Rocks and Cat Cay.

Fig. 9. Concentration of soluble iron in the Florida Current (From Corcoran 1967).

greatest tropical sport fishing regions are located where blue-water brushes land masses. These include the "edges" of the Florida Current off southeast Florida and Bimini, the blue-water of Hawaii, the north coast of Puerto Rico, Bermuda and the Challenger banks, and the Pacific coast of western Mexico off Acapulco and Baja California. Miami charter boat captains spend 90 percent of their trolling time along the "edge" where the blue waters of the Florida Current change horizontally within a few meters to the green water over-lying the coral reefs.

Some of this increased biomass of the blue-water coast is supported by the primary production of inshore reefs and seagrass covered bays. In many cases entire trophic levels are bypassed since pelagic fishes are able to feed upon benthic forms which in turn feed directly upon benthic plants and detritus. The effect of such a shortened food chain is to provide more top carnivores with little increase in primary production.

ENERGY FLOW THROUGH THE COMMUNITY

To visualize the one-way flow of energy through a coastal blue-water community it is necessary to consider the following points:

(1) Most of the energy is fixed in the euphotic zone by phytoplankton. These organisms serve as the engine which drives the system.

(2) There is a small input of energy from inshore and estuarine primary production. This arrives offshore in the form of large particles (such as Thalassia leaves), small particles and dissolved organic matter.

(3) Inorganic and organic compounds are recycled very rapidly in the surface waters by phytoplankton, colorless flagellates and zooplankton with little assistance from bacteria and fungi (discussed at length by Johannes, 1968).

(4) There is a general downward movement of much of the primary production from the euphotic zone. This is accomplished by sinking of phytoplankton, zooplankton and fecal pellets. Perhaps, most important is the vertical diurnal migration by animals from below which speeds up the downward movement of organic matter.

Energy transfer to the consumer trophic levels of oceanic systems is poorly understood. Blackburn (1966) has estimated the relationships existing between the standing crops of three successive trophic levels in the eastern tropical Pacific. The ratio between copepods and phytoplankton was estimated by weight of carbon while that between the carnivores and zooplankton was derived from displacement volume. Both relationships were roughly 0.04. For various reasons it was concluded that the actual efficiency ratios of the food chain for standing crops of all material at the appropriate trophic levels would be higher.

Certainly, more data are needed, although it becomes more and more difficult to make any type of meaningful estimation at the higher trophic levels since the consumers become more non-selective in their choice of foods. The yellowfin tuna, which is considered to be a top carnivore, has been recorded to ingest species from at least 12 orders of invertebrates and 44 families of fishes (Alverson, 1963).

WASTES AND BLUE-WATER COASTS--A BOTTOMLESS GARBAGE CAN?

". . . the high piled scow of garbage, bright-colored, white-flecked, ill smelling, now tilted on its sides, spills off its load into the blue water, turning it a pale green to a depth of four or five fathoms as the load spreads across the surface, the sinkable part going down and the flotsam of palm fronds, corks, bottles, and used electric light globes, seasoned with an occasional condom or a deep floating corset, the torn leaves of a student's exercise book, a well-inflated dog, the occasional rat, the no-longer distinguished cat,. . . the stream with no visible flow, takes five loads of this a day when things are going well in La Habana and in ten miles along the coast it is clear and blue and unimpressed as it was ever before the tug hauled out the scow . . ." Hemingway (1935).

Clearly, the blue-water coast with its association with open ocean systems offers an attractive solution to a society which is rapidly producing more and more waste products. There is a feeling as expressed in the passage above of the infinite ability of the sea to absorb all of man's capacity to manufacture garbage and sewage. This is a common and widespread feeling. It might be pointed out that at the turn of the century there was another commonly accepted theory about the sea--that it was an inexhaustible source of food fishes. Let us hope that present feelings on waste disposal are not as erroneous!

There are indications that it may not be possible to pollute the open ocean without some adverse feedback from the system. Pearcy and Osterberg (1968) have recently demonstrated that very small concentrations of ^{65}Zn carried down the Columbia River from the Hanford reactors and into the North Pacific have become concentrated to significant levels in the popular food and gamefish, the albacore Thunnus alalunga. Moreover, radionuclides from the same source have been found in many marine organisms off Oregon (Osterberg, Pearcy and Curl, 1964; Pearcy and Osterberg, 1967; Carey, Pearcy and Osterberg, 1966b).

Even more startling is the finding by Wurster and Wingate (1968) of dangerous levels of DDT and its metabolites in the Bermuda Petrel. This is highly interesting since this bird feeds only in the open ocean regions of the North Atlantic. It is at first difficult to conceive of such an organism obtaining potentially lethal amounts of DDT from an area so far removed from pesticide application.

The effects of sewage disposal on blue-water coasts are not at all clear. Along the southeast coast of Florida there are a number of sewer outfalls which dump raw or partially treated sewage directly onto the edge of the Florida Current. From this practice three questions have arisen: (1) what are the effects of sewage enrichment upon the blue-water system--great effects might be expected since this is a stable low nutrient environment--(2) how much of the material finds its way back to shore by means of inshore eddies and (3) what is the fate of potentially dangerous microorganisms in the effluent? The questions remain unanswered, but investigations are underway at Florida Atlantic University at Boca Raton.

Economical Importance of Blue-Water Coasts

A primary value of blue-water coasts is to the fisherman--especially the sportfisherman. Florida, Puerto Rico and Hawaii all have large sportfishing fleets which employ many people and combined are worth millions of dollars annually. These fleets are dependent to a great extent upon the pelagic fishes of the open ocean and to a lesser extent upon reef and inshore fishes.

Many other fishermen and boats use the blue-water regions on a part time basis for recreation. These amateur fishermen number in the thousands. On a weekend it is not unusual to see hundreds of private and charter fishing boats along the edge of the Florida Current between West Palm Beach and Miami. Any consideration of the future effects of pollution on the blue-water coasts should take as its first priority the effects on the commercial and gamefish stocks.

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